Contribution de différents éléments forestiers et non-forestiers de la trame de très vieux bois à la diversité des coléoptères saproxyliques

Guilhem Parmain

UNIVERSITÉ D'ORLÉANS

ÉCOLE DOCTORALE SANTE, SCIENCES BIOLOGIQUES ET CHIMIE DU VIVANT

Equipe biodiversité, IRSTEA Nogent-sur-Vernisson

THÈSE présentée par :

Guilhem PARMAIN

soutenue le : **22 Janvier 2015**

pour obtenir le grade de : **Docteur de l'université d'Orléans**

Discipline/ Spécialité : Biologie Forestière

Contribution de différents éléments forestiers et non-forestiers de la Trame de Très Vieux Bois à la diversité des coléoptères saproxyliques

THÈSE co-dirigée par :

Frédéric GOSSELIN : Ingénieur-Chercheur IRSTEA EFNO (Nogent/Vernisson)
Christophe BOUGET : Ingénieur-Chercheur IRSTEA EFNO (Nogent/Vernisson)

RAPPORTEURS :

Hervé BRUSTEL : Enseignant-chercheur Ecole d'Ingénieurs de PURPAN (Toulouse)
Julien PETILLON : Maitre de conférences Université de Rennes (Rennes)

JURY *(y reporter tous les membres de jury présents à la soutenance)*:

Hervé BRUSTEL : Enseignant-chercheur Ecole d'Ingénieurs de PURPAN (Toulouse)
Julien PETILLON : Maitre de conférences Université de Rennes (Rennes)
Christophe BOUGET : Ingénieur-Chercheur IRSTEA EFNO (Nogent/Vernisson)
Guillaume DECOCQ : Professeur de l'Université de Picardie Jules Verne (Amiens)
Marc DECONCHAT : Directeur de recherches DYNAFOR (Castanet Tolosan)
François LIEUTIER : Professeur de l'Université Orléans (Orléans)

Remerciements

Ce travail de recherche, cette aventure scientifique et personnelle n'a pu être possible que grâce à l'aide et au soutien de nombreuses personnes et structures.

Merci (et il est grand dans le cœur, même s'il est court dans le propos) :

aux financeurs, l'ONF, le Ministère de l'écologie, le Muséum d'Histoire Naturelle de Paris et IRSTEA,

à Albert Maillet et Michel Hermeline qui ont activement œuvré pour la mise en place du co-financement ONF,

à Sabine Moreau, Julien Tourroult, Vincent Boulager pour avoir été les représentants des structures partenaires, et m'avoir prodigué conseils et idées d'expérimentation, d'analyses,

à Christophe Bouget, pour avoir proposé et encadré ce projet de recherche,

à Thierry Noblecourt, et Patrice Hirbec pour avoir géré les conflits que ce travail a pu générer, ainsi que des préoccupations administratives qui m'ont évité bien des tracas,

aux membres du jury qui ont accepté de juger mon travail produit sur ces trois années,

aux membres de mon comité de thèse qui par leurs conseils ont permis de faire évoluer des réflexions embryonnaires en expérimentations concrètes,

à Frédéric Gosselin, pour ces précieux conseils d'analyses statistiques,

au personnel ONF impliqué, pour m'avoir fait découvrir leurs forêts, les petites zones cachées que seul le passionné connait, et qui sont également devenues un peu 'mes' forêts,

au réseau national d'Entomologie Forestière de l'ONF et au Laboratoire National d'Entomologie de l'ONF pour leur aide à l'identification de familles particulièrement ardues au sein des Coléoptères. Je n'oublierai pas de remercier ici les différents spécialistes qui ont bénévolement participé à l'identification de familles orphelines : Gianfranco Liberti (Dasytidae), Benjamin Calmont (Ptininae), Yves Thieren et Christian Perez (Pselaphidae ; Scydmaenidae), Yves Gomy (Histeridae).

aux différents propriétaires privés dans l'Allier qui ont eu l'amabilité de me laisser accéder à leurs terres et étudier la faune singulière des arbres isolés,

à Carl, pour le coup de main sur le terrain mais aussi à la conduite,

au personnel (permanent ou temporaire) ONF de Quillan et de l'IRSTEA de Nogent sur Vernisson pour leur accueil et leur bonne humeur, les conversations constructives autour d'un thé, et les moments de détente au badminton,

aux amis et à la famille, qui par leurs encouragements, leur soutien et leur bonne humeur m'ont aidé à mener ce travail à bon port. J'ai été un peu moins disponible ces derniers temps, mais je ne vous oublie pas…

Sommaire

Table des tableaux (Hors articles)

Table des figures (Hors articles)

Table des cartes (Hors articles)

Introduction générale

Introduction générale

I) Les forêts, sources importantes de biodiversité fortement impactées par l'activité humaine

Les forêts sont parmi les écosystèmes les plus riches de la planète (Larrieu et Gonin, 2008). Au cours des 300 dernières années, les forêts mondiales ont perdu environ 40 % de leur surface. Elles ont complètement disparu dans 25 pays et 29 autres pays ont perdu plus de 90 % de leur couverture forestière, et ce déclin se poursuit encore actuellement (FAO, 2012).

I.1) Les forêts en Europe

En Europe, la forêt recouvrait environ 80% de la surface du territoire à la fin de la dernière grande glaciation (environ -10000 ans, le Würm). Actuellement, ce couvert forestier n'est plus que de 45% (FAO, 2011). De plus, environ 99% de la surface des forêts présentes à la fin du Würm ont été impactées par l'activité anthropique (Gilg, 2004). L'Europe est la région du monde la plus diversifiéeen types forestiers forêts (FAO, 2011). Elles y présentent une grande variété, en passant par des toundras de Sibérie aux forêts méditerranéennes, ou par les grandes chênaies de plaine, les hêtraies-sapinières de montagne, sans oublier les forêts de pins à crochet d'altitude. Elles font également l'objet d'un prélèvement intensif de bois. En Europe, les forêts ont été exploitées depuis des millénaires (Grove, 2002a). Cette exploitation a conduit à la raréfaction (sinon à la disparition) des structures caractéristiques des forêts à caractère naturel (ou old-growth forests) (Gilg, 2004).

I.2) Caractéristiques structurelles des « Old-Growth Forests »

Le terme « Old-Growth Forest » (OGF) désigne une forêt à vieux peuplements, structurellement non impactée par l'activité humaine. Cette dénomination ne véhicule pas forcément une notion de continuité forestière, contrairement au terme anglo-saxon de « *ancient woodland* » (Kirby *et al.,* 1995). Les OGF présentent des éléments structurels singuliers, absents ou rares dans les forêts exploitées. Les OGF sont généralement composées de peuplements avec une grande diversité d'essences d'arbres, créant une structuration verticale complexe. La dynamique forestière est constituée de plusieurs phases. Ces phases sont entremêlées au sein des forêts naturelles, impliquant une composition en âge des arbres non uniforme au sein des peuplements. Plusieurs stades de développement d'une même essence seront alors présents dans les mêmes peuplements. Au fur et à mesure de l'augmentation de l'âge des arbres, leur probabilité de subir des évènements catastrophiques (incendies, tempêtes) va augmenter. Ces évènements induisent des blessures sur les branches ou le tronc, auxquelles l'arbre peut survivre. Ces blessures vont constituer les points d'entrée d'organismes décomposeurs de bois (principalement des Mycètes (Alexander, 2008)) et former des structures particulières, telles des plages de bois dur, des cavités... Ainsi, avec l'âge, un arbre va présenter une probabilité accrue d'acquérir de telles 'blessures'. Larrieu et Cabanettes, (2012) ont constaté que les arbres de fort diamètre avaient une probabilité accrue d'être porteurs de dendromicrohabitats.

Lors des phases finales du cycle de la sylvigenèse, les arbres des essences dominantes vont devenir sénescents puis mourir. Ces arbres morts vont rester sur place, debout ou au sol et constituer d'importants volumes de bois mort (Bobiec, 2002). Le bois mort est constitué d'une grande variété d'éléments, en passant des petites branches fraichement mortes aux futs d'arbres morts il y a plusieurs dizaines d'années et en état de décomposition avancée.

Les Old-Growt Forests sont structurellement plus complexes que les forêts exploitées. De même, elles possèdent des volumes et diversité de bois vivants et morts plus importantes. Enfin, la quantité et la diversité des dendromicrohabitats y est plus importante (Spies et Franklin, 1988 ; Sippola et al., 1998 ; Siitonen et al., 2000 ; Siitonen, 2001).

II) Enjeux de conservation associés aux organismes saproxyliques

II.1) Principales causes de l'érosion de la biodiversité forestière

La disparition d'habitat et la fragmentation du milieu sont deux processus distincts (Fahrig, 2003) et constituent des problématiques liées à l'écologie du paysage. La première définition de l'écologie du paysage a été fournie par Carl Troll en 1939. L'écologie du paysage est alors décrite comme « *l'étude des principales relations entre les communautés et leur environnement* » (Troll, 1939). Cette définition a été implémentée au fur et à mesure du temps, mais ce concept en reste le fondement. Actuellement, l'écologie du paysage est appréhendée comme une science à part entière, clairement pluridisciplinaire (Turner, 2005 ; Wu, 2006).

II.1.1) Disparition d'habitat

L'habitat d'une espèce ou d'une communauté d'espèces est délimité dans l'espace. Cet habitat peut avoir des tailles différentes en fonction des organismes considérés. Ainsi, un lynx ou un ours ont besoin de grandes étendues de forêts non perturbées par l'activité humaine pour pouvoir survivre (Ruggiero *et al.,* 1994 ; Schoen, 1990). D'autres organismes auront besoin de surfaces plus faibles, mais il existe une surface minimale d'habitat -propre à chaque espèce- en deçà de laquelle les populations ne peuvent se maintenir (Andrén, 1994). Deux principales configurations spatiales de distribution de l'habitat sont générées par sa disparition. Dans un premier cas, le nombre d'éléments d'habitats dans le paysage reste constant (Figure 1a). Dans le deuxième cas, le nombre d'éléments d'habitat varie dans le paysage. Le nombre d'éléments d'habitat dans le paysage peut soit augmenter (Figure 1b), soit diminuer (Figure 1c).

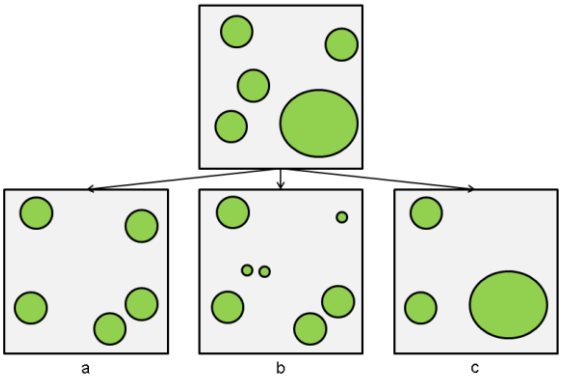


Figure 1 : Différentes conséquences de la disparition d'habitat sur le nombre de patches d'habitat restants.

Dans le cas où les éléments d'habitat dans le paysage varient en nombre, on aboutit à une variation du degré de fragmentation spatiale de l'habitat.

II.1.2) Fragmentation d'habitat et réduction de connectivité

La fragmentation spatiale d'habitat ne traduit pas systématiquement une perte d'habitat (Fahrig, 2003). Un large patch d'habitat peut être scindé en deux patches distincts pour une même surface totale. Dans ce cas, si la distance inter-patches est inférieure à la distance de dispersion de l'espèce considérée, et que la matrice inter-patch permet la dispersion (Baum *et al.,* 2004), les deux patches sont considérés comme connectés. Les processus de disparition ou de fragmentation de l'habitat vont créer un réseau plus ou moins connecté de patches de tailles variables. Au sein des forêts, les structures caractéristiques des OGF ne se répartissent pas de manière uniforme. Certaines zones peuvent en effet présenter des volumes et une diversité de bois mort plus importantes que d'autres, suite à une perturbation naturelle (tempête, incendie). De la même façon, les arbres porteurs de dendromicrohabitats ne vont pas être répartis de manière continue au sein de la forêt. On aboutit alors à des structures d'habitat mosaïques (Gilg, 2004).La configuration spatiale discontinue des compartiments « bois mort » et « dendromicrohabitat » au sein des forêts va induire une dynamique de population particulière, la métapopulation. Il est important de préciser que la fragmentation n'a pas toujours des effets négatifs sur les organismes (Fahrig, 2003, Bouget et Duelli, 2004), en particulier pour les espèces à fort pouvoir de dispersion (MacInerny *et al.,* 2007). C'est par exemple le cas pour la chenille processionnaire du Pin. Son front de dispersion actuel vers le Nord de la France est accéléré par une structure spatiale fragmentée (arbres isolés, alignements le long des autoroutes) de son habitat (les pins) plutôt que non fragmentée (patches de forêt).

II.1.2.Réponse des populations à la fragmentation de l'habitat

Une population peut se définir comme un « *ensemble d'individus d'une même espèce occupant une niche dans une biocœnose* » (Arnaud et Amig, 1986). Une métapopulation est un niveau d'organisation particulier de certaines populations au sein d'une même aire géographique. Le concept est hérité des recherches sur la théorie des iles de MacArthur et Wilsson (1967). Bien qu'ils aient initialement étudié des communautés végétales sur des iles, les concepts ont rapidement été transposés aux écosystèmes terrestres continentaux qui présentaient une répartition spatiale fragmentée mais connectée. Une métapopulation est composée à l'échelle du paysage de populations locales occupant des patches d'habitat. Ces populations sont de tailles diverses et

peuvent présenter des risques élevés d'extinction locale, en fonction des capacités d'accueil de l'habitat. Ainsi, certains patches d'habitat vont permettre la survie de populations. Au contraire, d'autres vont voir la population qu'ils abritent décliner puis s'éteindre. Ces patches d'habitat alors non occupés pourront être recolonisé par la suite, s'ils redeviennent des habitats favorables. Ils seront recolonisés par les individus en provenance de patches voisins. Le tout forme à l'échelle du paysage et du temps un réseau dynamique d'extinctions et de colonisations. Les mécanismes régissant les métapopulations et la façon d'appréhender leur fonctionnement font encore débat aujourd'hui (Baguette, 2004 ; Hanski, 2004). Malgré cela, l'utilisation de modèles métapopulationnels a permis la mise en place de mesures conservatoires favorables à nombreuses espèces (Akçakaya *et al.,* 2007).

Il est important de noter que c'est l'habitat qui va structurer le fonctionnement de populations en métapopulations, et qu'en fonction de l'échelle spatiale et temporelle considérée, toutes les populations d'êtres vivants sont susceptibles de se comporter en systèmes métapopulationnels.

II.1.2.2) Effets de débordement d'individus (Spillover)

Dans un habitat favorable, la théorie veut que les populations d'organismes se développent jusqu'à atteindre des seuils populationnels trop importants pour être maintenus dans la zone considérée. Les individus surnuméraires vont alors disperser vers les zones voisines, en addition des effets de dispersion classiques. Cet apport d'individus surnuméraires dans des zones voisines à partir de zones plus riches est appelé effet spillover, ou effet de débordement. Cet effet a été étudié dans de nombreux écosystèmes (Brudvig *et al.,* 2009 ; Russ et Alcala, 2011 ; Lucey et Hill, 2012).

II.2) Effets de l'exploitation sur la structure des forêts

II.2.1) Dynamique naturelle des forêts …

II.2.1.1) Sylvigenèse

Gilg (2004) a proposé une synthèse du cycle sylvigénétique des forêts d'Europe laissées en libre évolution. Sa synthèse se base majoritairement sur les recherches de Jones (1945) et Oldeman (1990). Le cycle sylvigénétique varie quelque peu en fonction des essences et contextes mais reste globalement le même (Vera, 2000) et applicable aux forêts que nous avons étudiées. De manière générale, deux types de cycles sylvigénétiques sont admis, basés sur l'intensité des perturbations naturelles auxquels ils sont soumis. Dans le premier cas, le cycle sylvigénétique dit « à dynamique douce », et dans un second temps, le cycle sylvigénétique dit « à dynamique catastrophique ».

II.2.1.1.1) Le principe d'éco-unité

Le principe « 'd'éco-unité » est introduit par Oldeman (1990). Il correspond à l'unité élémentaire de développement de la forêt, celle au sein de laquelle va se dérouler le cycle sylvigénétique. En fonction des dynamiques forestières, cette éco-unité peut varier d'une surface de quelques dizaines de mètres de rayon en dynamique douce à plusieurs centaines en dynamique catastrophique (Gilg, 2004). A l'échelle de la forêt, plusieurs éco-unités vont exister simultanément, parfois côte à côte, parfois imbriquées les unes dans les autres. Il en résulte un paysage mosaïque.

II.2.1.1.2) La sylvigenèse douce

Dans une dynamique forestière douce, non soumise à des perturbations naturelles de grande ampleur, trois stades principaux vont être facilement identifiables : Un stade de croissance et de développement des peuplements (accroissement), un stade de stabilisation (optimal) et un stade de rajeunissement (régénération) par écroulement des arbres les plus âgés (Gresslier *et al.,* 1995). Durant le stade d'accroissement, les arbres mourants ou morts de la fin du cycle précédent vont coexister avec la régénération des semis du nouveau cycle en cours. S'en suit une phase stable, qui caractérise le stade optimal (Gilg, 2004). Il est caractérisé par la croissance jusqu'à maturité des arbres issus du stade précédent. Le déclin des arbres matures du stade optimal et le début de l'installation de nouveaux semis marquent le début du stade de régénération. Des phases intermédiaires peuvent être ajoutées à ce cycle et sont détaillées Figure 2.

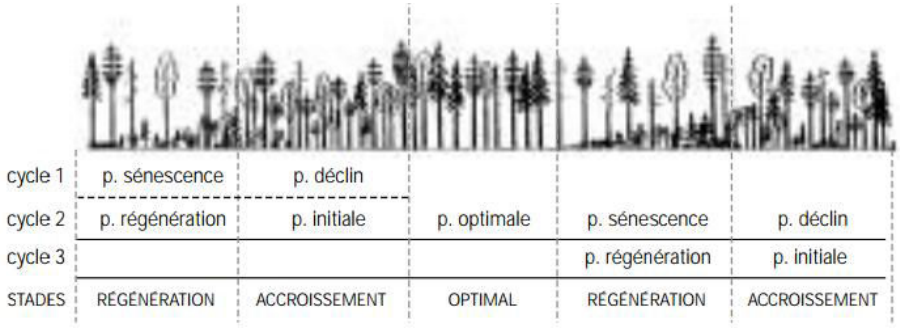


Figure 2 : Sylvigenèse à dynamique douce telle qu'observée en hêtraie-sapinière (Korpel, 1995 in Gilg, 2004).

II.2.1.1.3) La sylvigenèse avec évènements catastrophiques

La dynamique forestière de type « catastrophique » inclue dans le cycle sylvigénétique classique des évènements catastrophiques de grande ampleur. Ces évènements catastrophiques sont majoritairement constitués par les tempêtes et les incendies. Ils vont provoquer de larges troués au sein des forêts, et « réinitialiser » le cycle sylvigénétique. Il faut alors que la forêt recolonise les zones ainsi perturbées. Cette recolonisation va se faire par des essences héliophiles. Ces essences qui ne nécessitent pas de couvert forestier pour se développer sont nommées essences pionnières. Une fois un stade de développement suffisant atteint, les essences forestières sciaphiles vont se développer et un nouveau cycle sylvigénétique va se mettre en place (Figure 3). Une forêt peut posséder les deux types de sylvigenèse en fonction de l'intensité des perturbations, mais une des dynamiques est généralement dominante (Gilg, 2004). Il est important de noter que la catastrophe qui va réinitialiser le cycle peut se produire à n'importe quel moment du cycle.

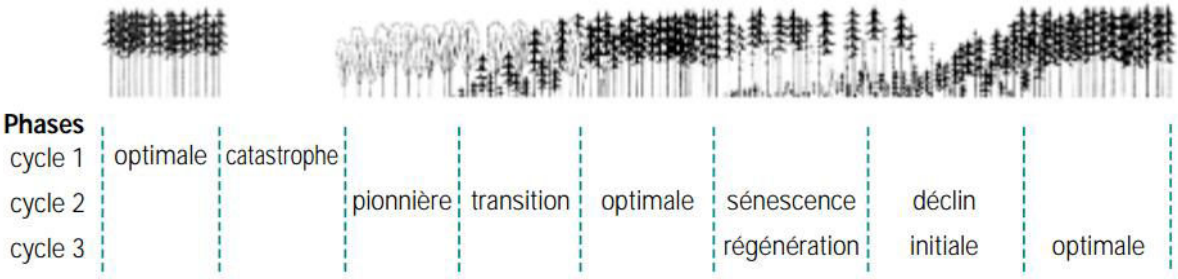


Figure 3 : Sylvigenèse de type catastrophique, typique des écosystèmes forestiers boréaux (Schuck *et al.,* 1994 in Gilg, 2004).

II.2.2) Dynamique en zones exploitées

Les peuplements forestiers peuvent être traités de plusieurs façons, en fonction des objectifs de production associés (Dubourdieu, 1997). Sommairement, deux types de traitements sont utilisés : la futaie et le taillis. Les deux traitements peuvent être utilisés en même temps pour aboutir à un traitement de taillis sous futaie (Perrin, 1946). La futaie a pour objectif la production de bois de grande qualité, destiné à la construction, tonnellerie, ébénisterie en fonction des essences considérées. Ce traitement est caractérisé par les longues périodes nécessaires à l'obtention de tels bois. Au contraire de la futaie, le taillis est destiné à produire rapidement du bois de faible diamètre. Anciennement utilisé pour produire du bois de chauffage, il est de plus en plus utilisé pour les besoins de la filière bois énergie. Le taillis est caractérisé par des périodes de rotation courtes. Du fait des durées de rotations différentes entre ces deux traitements, la sylvigenèse naturelle (Figure 4a) ne sera pas impactée aux mêmes phases. Dans le cas de la futaie, les arbres seront récoltés en phase optimale du cycle, là où leur vitesse de croissance va diminuer, et le risque de dépréciation économique augmenter par l'apparition d'imperfections (*i.e* les dendro-microhabitats) (Figure 4b). Dans le cas du taillis, les arbres sont récoltés durant la phase de croissance, avant qu'ils n'atteignent la phase optimale (Figure 4c). La récolte des arbres à différents stades du cycle sylvigénétique tronque ce dernier dans les phases critiques de développement des habitats favorables aux espèces saproxyliques. Ainsi, les phases de sénescence et de déclin sont généralement absentes des forêts exploitées.

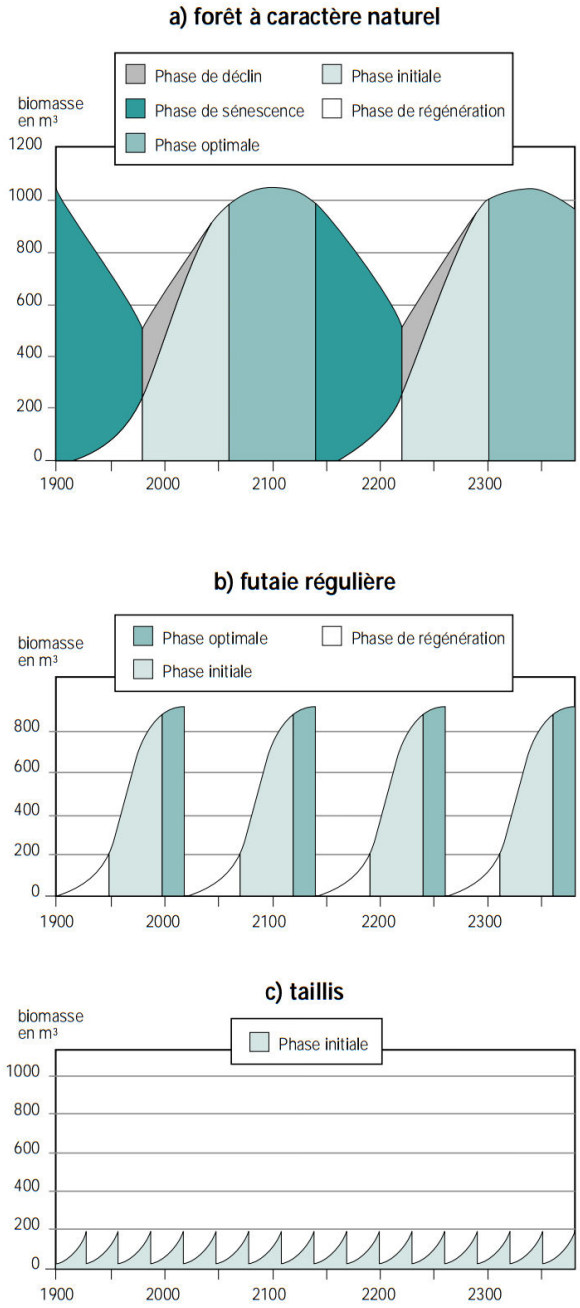


Figure 4 : Impact du mode d'exploitation forestière sur la dynamique naturelle de la sylvigenèse (d'après Gilg, 2004). Les phases de sénescence et de déclin sont absentes des forêts exploités.

L'exploitation forestière modifie significativement la structuration des peuplements forestiers (Parrotta *et al.,* 2002 ; Maguire *et al.,* 2007 ; Angers *et al.,* 2005 ; Linder *et al.,* 1997). Le volume d'arbres vivants est moins important dans les zones exploitées (Siitonen *et al.,* 2000). La structuration verticale de la végétation est simplifiée (Sturtevent *et al.,* 1996) et la composition floristique change fortement (Halpern et Spies, 1995). La quantité et la diversité de dendromicrohabitats est également diminuée dans les zones exploitées par rapport aux zones non exploitées (Larrieu *et al.,* 2012), ainsi que le volume et la diversité du bois mort (Fridmann et Walheim, 2000 ; Rahman *et al.,* 2008). Cette diminution est accentuée par l'élimination générale des arbres porteurs de dendromicrohabitats, car économiquement dépréciés.

II.2.2.1) Le cas particulier des compartiments « bois mort » …

En retirant du cycle sylvicole naturel les arbres qui auraient dû mourir et se décomposer sur place, l'exploitation forestière affecte largement la dynamique du bois mort en forêt (Fridmann et Walheim, 2000). Rahman *et al,* (2008) ont étudié l'effet de l'exploitation forestière dans une forêt de chênes en Autriche. La quantité de bois mort retrouvée sur les placettes exploitées est bien moindre que celle retrouvée sur les parcelles non exploitées. Martikainen *et al,* (2000) ont étudié trois niveaux d'intensité d'exploitation forestière en Finlande, dans des forêts d'épicéa. Au fur et à mesure que le cycle d'exploitation est rallongé (que l'intensité d'exploitation diminue), le volume de bois mort augmente. On peut ainsi constater une augmentation de 750% du volume de bois mort moyen entre les parcelles avec un âge d'exploitation faible (90/120 ans) et les parcelles non exploitées (depuis plus de 160 ans) ! Moroni et Ryan (2010) fait la même constatation en Nouvelle Ecosse, dans les forêts de feuillus. De nombreuses autres études ont mis en évidence la diminution du volume de bois mort dans des parcelles exploitées par rapport à des parcelles non exploitées (Kirby *et al.,* 1991; Sippola *et al.,* 1998 ; Boncina, 2000; Marage et Lempérière, 2005; Sitzia *et al.,* 2012).

Le compartiment « bois mort » n'est cependant pas impacté de manière uniforme. En effet, le volume de bois mort total est composé de nombreux éléments : le bois mort debout ou au sol, de petit ou gros diamètre, fraichement mort non décomposé, ou mort et fortement décomposé... En Autriche, Rahman *et al,* (2008) ont montré que la diversité de bois mort était plus faible dans les zones exploitées que non exploitées. Moroni et Ryan (2010) ont montré que le bois fraichement mort de petit diamètre est plus abondant dans les zones exploitées que non exploitées. Green et Peterken (1997) ont trouvé que les gros bois morts sont plus rares dans les zones exploitées que les zones non exploitées depuis au moins 100 ans. Lohmus *et al,* (2005) ont pour leur part trouvé plus de gros bois mort au sol dans les zones exploitées que dans les zones en réserve. Ils expliquent ce phénomène par les coupes à blanc qu'ont subies les réserves forestières en Estonie il y a moins de 200 ans.

Il faut également prendre en compte les traitements post-exploitation qui peuvent encore plus diminuer le volume de bois mort restant. Il peut en effet y avoir la récolte des rémanents pour la filière bois énergie (Ranius *et al.,* 2014 ; Rudolphi et Gustafsson, 2005 ; Bouget *et al.,* 2011), ou le broyage des rémanents et l'arrachage des souches (Miklin et Cizek, 2014). Le volume de bois mort restant est alors réduit de manière drastique.

De manière générale, le volume de bois mort dans les parcelles non exploitées semble être similaire en Europe et en Amérique (Nilsson *et al.,* 2003), et est bien supérieur au volume retrouvé dans les

zones exploitées (Fridmann et Walheim, 2000 ; Christensen *et al.,* 2005). Naturellement, la régénération des stocks de bois mort est un processus lent (Vandekerkhove *et al.,* 2009), mais conduisant à des volumes et une diversité constante au sein des différentes phases de la sylvigenèse (Larrieu *et al.,* 2014).

En plus d'être un habitat primordial pour la survie de nombreuses espèces (Nordén *et al.,* 2004), le bois mort assure plusieurs rôles fonctionnels (Stokland *et al.,* 2012) : la protection des sol de l'érosion, son rôle protecteur vis-à-vis des chutes de blocs en montagne (Bigot, 2014), l'influence sur le cycle de divers éléments (Laiho et Prescott, 1999 ; Holub *et al.,* 2001) ou encore la séquestration du CO_2 atmosphérique (Luyssaret *et al.,* 2008).

II.2.2.2) …et « dendromicrohabitats »

De manière simplifiée, l'habitat d'une espèce ou d'une population va regrouper tous les éléments structurels nécessaires à sa survie (Larrieu, 2014). Un microhabitat ne va pas forcément regrouper la totalité de ces éléments, mais en constitue un élément essentiel. C'est par exemple le cas des mares pour certains batraciens.

Dans le cas présent, nous employons le terme microhabitat dans le cadre précis des structures favorables à la biodiversité des espèces forestières portées par les arbres (vivants ou morts). Ils peuvent alors être regroupés sous le terme de dendromicrohabitats (Larrieu, 2014). La bibliographie disponible sur le sujet est peu nombreuse, et un travail récent en fait la synthèse (Larrieu, 2014). Un dendromicrohabitat peut par exemple être une cavité d'arbre, un champignon du bois, du bois mort dans le houppier ou encore de larges plages de bois sans écorce ou plages d'écorce décollées du tronc (Michel et Winter, 2009 ; Larrieu et Gonin, 2008).

La probabilité d'occurrence des dendromicrohabitat est plus grande sur les arbres de plus fort diamètre (Larrieu et Cabanettes, 2012 ; Winter et Möller, 2008). Larrieu *et al,* (2012) ont montré que dans des forêts de hêtraie sapinière dans les Pyrénées, le nombre et la diversité en dendromicrohabitats étaient plus importants en zone non exploitée qu'en zone exploitée. L'exploitation forestière, en sélectionnant et retirant les arbres du cycle naturel de la forêt impacte donc profondément la quantité et la diversité des dendromicrohabitats disponibles (Michel et Winter, 2009). On peut s'attendre à avoir plus de dendromicrohabitats (quantité et diversité) dans les stades terminaux de la sylvigenèse que dans les stades pionniers. Pourtant, Larrieu *et al,* (2014) ont constaté que la quantité et la diversité en dendromicrohabitats étaient globalement identiques entre les différentes phases naturelles de la sylvigenèse.

Récemment, Vuidot *et al,* (2011) ont montré que la quantité et la nature des dendromicrohabitats n'était pas la même en fonction des types forestiers étudiés. Certaines essences d'arbres sont plus à même de porter des dendromicrohabitats que d'autres, comme le chêne ou le hêtre, plutôt que le sapin. Le chêne est particulièrement reconnu comme pourvoyeur de dendromicrohabitats d'une grande valeur écologique et d'une grande stabilité temporelle (Ranius et Nilsson, 1997 ; Gouix et Brustel, 2012).

Les OGF possèdent des compartiments « bois mort » et « dendromicrohabitats » particulièrement riches et diversifiés. En retirant du cycle naturel de la sylvigenèse des arbres qui auraient dû mourir et se décomposer sur place, l'exploitation forestière impacte fortement le compartiment bois mort. De même, les arbres présentant des dendromicrohabitats sont généralement retirés du cycle sylvigénétique naturel par l'exploitation, car facteurs d'une dépréciation économique du bois (ONF, 2009). Les espèces associées à ces deux compartiments sont victimes d'une diminution drastique de leur habitat au sein des forêts exploitées.

III) Biodiversité associée au bois mort et aux dendromicrohabitats

III.1) Impact de l'exploitation forestière sur la biodiversité associée au bois mort

III.1.1) Les organismes saproxyliques

Les organismes saproxyliques sont les espèces qui sont impliquées ou dépendent du processus de décomposition du bois par les champignons, ou du produit de cette décomposition, et qui sont associées aux arbres vivants comme morts. Il convient d'inclure deux groupes supplémentaire à la définition : i) les espèces associées aux coulées de sève et des produits de sa décomposition, et ii) les organismes autres que les champignons qui consomment directement le bois. » Alexander (2008). Les espèces saproxyliques représentent environ 25% des espèces forestières en Scandinavie (Stokland *et al.,* 2004), et 20% en Grande-Bretagne (Elton, 1966 in Dajoz, 1998). De manière globale, un quart des espèces forestières est considérée comme saproxylique (Bouget, 2007).

Evolution du concept de saproxylisme

Les organismes dépendant du bois mort ou des dendromicrohabitats appartiennent à différents ordres mais peuvent tous être regroupés sous une appellation fonctionnelle identique : les espèces saproxyliques. Le terme a été concrétisé par Speight (1989). Il définit alors les invertébrés saproxyliques comme les « *espèces d'invertébrés qui sont dépendantes pendant une partie au moins de leur cycle vital, du bois mort ou mourant, debout ou au sol, ou de champignons du bois mort ou d'autres organismes saproxyliques* ». Cette définition première ne permet pas l'inclusion des champignons du bois, pas plus que les mousses, lichens ou chauves-souris forestières dans le groupe fonctionnel des saproxyliques. Cette inclusion n'est venue que plus tard. Une synthèse des réflexions menées autour du terme saproxylique lors du symposium international de Mantova a été produite par Anon (2003). Le terme saproxylique regroupe alors les organismes qui sont « *dépendants pendant une partie de leur cycle de vie du bois mort ou des arbres sénescents ou du bois au sol, ou d'autres organismes saproxyliques* ».

Selon Alexander (2008), le rôle primordial des champignons dans le cycle de décomposition du bois mort et le caractère facilitateur sinon obligatoire à l'installation d'autres espèces n'est pas suffisamment pris en compte. De même, le rôle des structures de bois mort ponctuelles sur des arbres vivants (cavités, plages de bois sans écorce) n'est pas intégré. Il propose alors la définition retenue ci-dessus.

L'évolution de la définition du terme saproxylique est récente et englobe une large gamme d'espèces. Il est dans certains cas délicat de juger du caractère saproxylique d'une espèce. En effet, il est des compartiments du bois mort qui sont à la frontière d'autres compartiments (tel le compartiment de la faune du sol). Certaines espèces vont se développer dans le bois mort au sol fortement décomposé. Mais est-ce là encore du bois mort ? La limite entre bois mort et humus est parfois délicate à définir. L'humus forestier est certes majoritairement composé de produits ligneux ou cellulosiques, mais ne peut être considéré comme du bois mort. Il faut donc user de prudence quant à l'affectation au groupe fonctionnel des saproxyliques, et savoir fixer des limites. Cet exercice est rendu d'autant plus difficile au vu du comportement trophique méconnu de nombreuses espèces (Bouget *et al.,* 2005).

Les espèces saproxyliques sont dépendantes des phases de sénescence et de déclin du cycle sylvigénétique naturel. Les forts volumes de bois mort ainsi que les arbres porteurs de dendromicrohabitats sont des structures clés permettant leur conservation (Stokland *et al.,* 2012 ; Krauss et Krumm, 2013). Ces compartiments sont particulièrement affectés par l'exploitation forestière. La diminution de volume et de diversité du bois mort ainsi que du nombre de dendromicrohabitats correspond à la disparition et à la fragmentation spatiale de l'habitat des espèces saproxyliques.

En Europe, les espèces saproxyliques représentent environ 25% des espèces forestières. Deux groupes taxinomiques regroupent la moitié de ces espèces : les champignons (30%) et les coléoptères (20%) (Bouget et Brustel, 2009). En France, les coléoptères saproxyliques sont représentés par 2500 espèces et ont une large variabilité inter-spécifique du niveau d'exigence écologique (Bouget et al. 2005). Les exigences écologiques de ces espèces peuvent être faibles (l'espèce va pouvoir se développer dans plusieurs substrats, de nature différente) ou fortes (l'espèce ne peut se développer que dans un type bien précis de substrat, comme par exemple, les cavités basses d'arbres feuillus dans un état de développement avancées Gouix, 2011). Il faut ajouter à la notion d'exigences écologiques la notion de rareté des espèces. La rareté est due à plusieurs facteurs, qu'ils soient intrinsèques aux populations considérées (faible nombre d'individus), ou biogéographiques (i.e limite d'aire de répartition). Une bonne synthèse du concept de rareté des espèces de coléoptères saproxyliques est fournie par Brustel (2001).

Les coléoptères saproxyliques sont largement utilisés en Europe et dans le monde comme modèles biologiques pour évaluer l'impact des perturbations anthropiques (ou naturelles) sur la biodiversité forestière ou la pertinence de mesures conservatoires en forêt.

Les coléoptères sont des insectes holométaboles. Ils ont un cycle de développement complexe constitué de 4 stades (figure5).

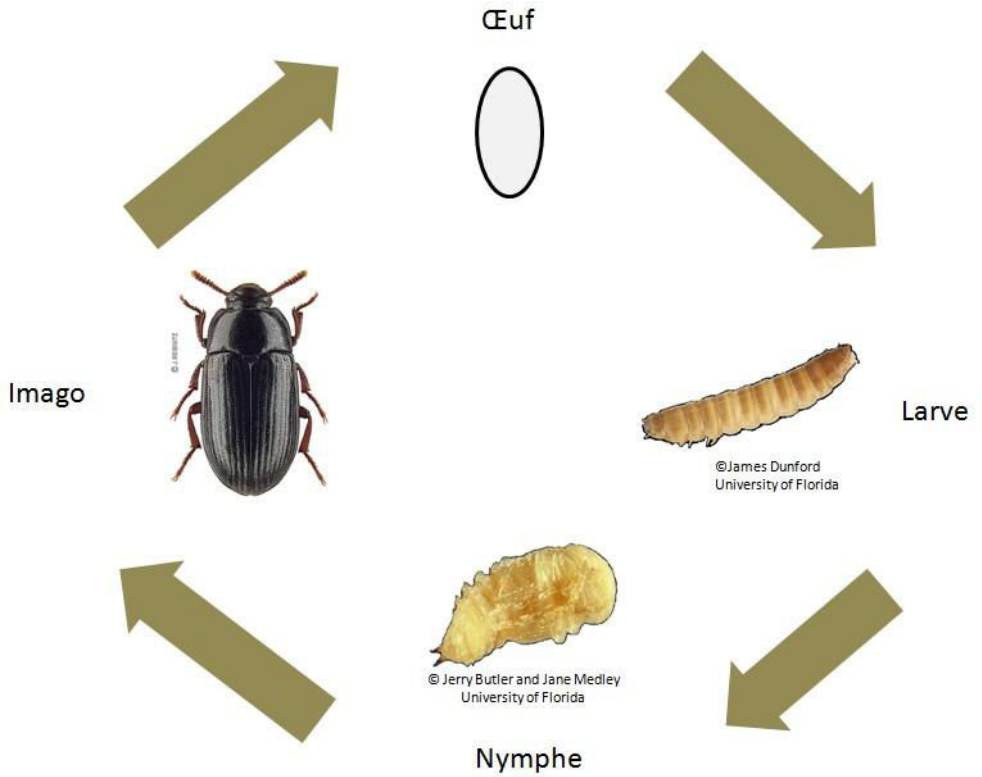


Figure 5 : Illustration du cycle de développement d'un coléoptère (Coleoptera, Tenebrionidae, *Alphitobius diaperinus*).

Le cycle de développement se déroule comme suit :

L'œuf est pondu par la femelle sur ou dans le substrat de développement des larves.

La larve s'extrait de l'œuf et va pénétrer dans son substrat de développement. Ce dernier est extrêmement diversifié et varie en fonction des espèces de coléoptères considérées. Il peut s'agir de bois fraichement mort (particulièrement apprécié par les Scolytidae, Cerambycidae), de bois carié (i.e décomposé par des champignons ; apprécié des Elateridae, Lucanidae...), de cavités d'arbres (appréciées des Cetoniidae), de fructifications de champignons saproxyliques (appréciées des Ciidae, Mycetophagidae) ... Au sein de ces milieux, les larves vont se déplacer et avoir des régimes trophiques variés en fonction des espèces. Elles peuvent consommer le substrat même, être prédatrices d'autres organismes ou encore commensales d'autres espèces saproxyliques. Les larves vont effectuer la totalité de leur développement dans le substrat, jusqu'à la nymphose. Cette étape du cycle est plus ou moins rapide en fonction des espèces et des conditions climatiques. Elle peut varier de quelques mois à plusieurs années.

La nymphe est une étape de métamorphose qui va permettre à la larve de devenir un imago. La nymphe ne se déplace pas dans le substrat, elle reste immobile durant sa transformation. La durée de cette étape du cycle est variable en fonction des espèces, mais généralement de l'ordre de quelques semaines.

L'imago issu de la nymphe va s'extraire du substrat pour se déplacer (par le vol ou la marche), rechercher de la nourriture (en fonction des espèces), un partenaire sexuel, se reproduire puis mourir. Tout comme les larves dont ils sont issus, les imagos vont présenter des régimes trophiques variés et parfois différents de celui de leurs larves (cf Bouget et al. 2005). Ils peuvent être aphages, (la totalité des réserves étant accumulée pendant leur développement larvaire), floricoles,

prédateurs... . La durée de ce stade du cycle est variable, pouvant aller de quelques jours à plusieurs mois.

Le stade de développement des coléoptères saproxyliques le plus pertinent pour étudier leur lien avec les stades matures des forêts est le stade larvaire. Il est possible d'associer précisément les espèces et leur substrat de développement. Cependant, aucune méthode standardisée de récoltes des larves n'est actuellement disponible. De plus, la récolte des larves implique une dégradation importante des substrats de développement larvaire. Enfin, l'identification des larves de coléoptères saproxyliques est particulièrement difficile, faute de documents et de compétences disponibles.

Le stade du cycle le plus utilisé pour l'étude des coléoptères saproxyliques en forêt –et retenu pour nos expérimentations- est l'imago. Des méthodes standardisées pour leur échantillonnage existent (Nageleisen et Bouget, 2009), la plupart n'impliquant pas la dégradation de leur habitat. Une littérature abondante est disponible pour l'identification de la plupart des familles. La possibilité d'avoir accès au réseau d'entomologistes national et extranational spécialisés sur les coléoptères saproxyliques est venue conforter notre choix.

III.1.2) Augmentation de la probabilité d'extinction

La quantité et qualité d'habitats disponibles influencent la probabilité d'extinction des populations (Ranius et Fahrig, 2006 ; Ranius et Kindvall, 2006). C'est par exemple le cas pour *Osmoderma eremita* (Coleoptera, Cetoniidae) qui vit dans les cavités d'arbres. Sa probabilité d'extinction augmente avec la diminution du volume des cavités (Ranius, 2007). Dans une approche par modélisation, Ranius et Roberge (2011) ont étudié la réaction de cinq espèces fictives toutes dépendantes de conditions écologiques particulières à la diminution de leur habitat. Dans tous les cas de figure, la probabilité d'extinction augmentait avec la diminution de l'habitat.

L'impact de l'exploitation forestière (disparition d'habitat et/ou fragmentation spatiale) sur les espèces saproxyliques qui y sont abritées ne suit pas toujours une relation linéaire. Des effets de seuils ont été mis en évidence pour plusieurs groupes taxinomiques (oiseaux, mammifères, insectes …) au sein de la communauté fonctionnelle des saproxyliques (Carlson, 2000 ; Roberge *et al.,* 2008 ; Bütler *et al.,* 2004 ; Reunanen *et al.,* 2004). En deçà d'une certaine quantité d'habitat dans le paysage, le déclin des populations considérées sera plus rapide que la perte d'habitat (Andrén, 1994, 1996). Toutes les espèces ne vont pas réagir aux mêmes seuils d'habitat. Certaines espèces ont besoin de plus d'habitat que d'autres pour assurer leur survie (Holland *et al.,* 2005) et les seuils de probabilité d'extinction des espèces ne seront donc pas les mêmes. Il faut noter que ces seuils de probabilité d'extinction dépendent des échelles spatiales et temporelles considérées (Engen *et al.,* 2002 ; Paltto *et al.,* 2006 ; Kuussaari *et al.,* 2009).

III.1.3) Diminution de la viabilité des populations à différentes échelles

Dans un habitat satisfaisant aux exigences écologiques des espèces qui y habitent, la démographie de ces espèces est stable, bien que possiblement cyclique (Maquet *et al.,* 2007). La disparition et la fragmentation de l'habitat va conduire à la diminution de la démographie des espèces considérées.

Dans le cas des espèces saproxyliques, cette relation entre disparition d'habitat et diminution de la démographie suit en général des relations à effets de seuils. Carlson (2000), Roberge *et al,* (2008), Virkkala *et al,* (1993) ont principalement étudié les pics. Les populations de pics sont en déclin dans les zones exploitées, et viables dans les zones non exploitées. Ces études ne se sont intéressées qu'à l'impact local de la disparition d'habitat sur la viabilité des populations. Dans le cas particulier des coléoptères saproxyliques, Martikainen *et al,* (2000) ont constaté que 78% des espèces qui étaient en commun entre zones exploitées et zones non exploitées présentaient des abondances plus importantes en zones non exploitées.

III.1.3.1) Le rôle de la densité d'habitat dans le paysage

Le cas particulier de l'écureuil volant de Sibérie illustre la nécessité de combiner deux niveaux d'approches spatiales (paysage et local) pour assurer la conservation des populations (Reunanen *et al.,* 2001). Cette espèce a besoin au sein du paysage de plusieurs types de ressources pour effectuer son cycle de vie. Ponctuellement, des zones avec des essences feuillues doivent être maintenues. Au niveau du paysage, une matrice forestière doit être assurée entre les différents patches de feuillus pour permettre le déplacement des individus entre ceux-ci (Reunanen *et al.,* 2001). Si certains de ces éléments venaient à faire défaut ou être en proportions insuffisantes, la viabilité des populations serait affectée (Reunanen *et al.,* 2001). L'importance de la considération d'échelles multiples pour la conservation des espèces a également été mise en évidence pour les communautés végétales. Cousins et Vanhohenaker (2011) ont par exemple mis en évidence que la survie locale des populations ne traduisait pas forcément la survie de l'espèce au niveau du paysage. Ainsi, l'étude des effets d'une perturbation à une échelle locale n'est qu'un aperçu de la totalité des processus en cours. Il est nécessaire de rappeler que la totalité du processus doit être appréhendé à diverses échelles spatiales. Ceci est également vrai pour les insectes (Roland et Taylor, 1997), et en particulier pour les coléoptères saproxyliques (Okland *et al.,* 1996 ; Holland *et al.,* 2004). Sahlin et Schroeder (2010) préconisent ainsi l'augmentation de la taille des ilots feuillus au sein de la matrice résineuse mais également l'accroissement de leur proportion dans le paysage pour augmenter la viabilité des populations d'espèces de coléoptères saproxyliques associées.

Pourtant, la mise en place d'études et de structures de conservation est plus généralement effectuée à l'échelle locale qu'à l'échelle paysagère (Schwartz, 1999).

III.1.3.2) Une réponse décalée dans le temps

L'échelle temporelle est également un paramètre clé pour assurer la conservation des espèces. Une modification brutale de l'habitat pourra par exemple n'avoir de conséquences sur la biodiversité qui en dépend que plus tard. C'est le concept de dette d'extinction (Kuussaari *et al.,* 2009). Cet effet stipule qu'une population peut subir les effets négatifs d'une perturbation de son habitat qu'après un délai. Ainsi, une réduction d'habitat peut ne pas influencer une population au moment ou elle intervient. En revanche, cette population verra ses effectifs diminuer jusqu'à disparaitre localement, alors que la quantité et la qualité d'habitat n'auront pas ou peu changé (Krauss et Krum, 2013). On appelle ces populations des 'living dead populations' (Bässler et Müller, 2010). Bien souvent, l'estimation du délai entre perturbation et extinction locale des populations est mal appréhendé (Jonsell, 2007 ; Sang *et al.,* 2010 ; Cousins et Vanhohenacker, 2011). Dans une approche de

modélisation, Ranius et Roberge (2011) ont estimé que les phénomènes d'extinction pouvaient prendre entre 50 et 150 ans.

III.1.4) Réduction du nombre d'espèces dans les communautés

III.1.4.1) Pool total d'espèces

La probabilité de survie des espèces forestières est affectée de manière négative par l'activité humaine. Si aucune mesure conservatoire n'est mise en place, des populations peuvent s'éteindre localement. De ce fait, les zones forestières exploitées devraient abriter moins d'espèces saproxyliques que les zones forestières non-exploitées. C'est ce qu'ont observé Martikainen *et al,* (2000) qui ont étudié la richesse spécifique en coléoptères de pessières exploitées et non exploitées en Finlande. Ils ont détecté un nombre d'espèces total différent entre les placettes exploitées et non exploitées, les placettes non exploitées présentant la plus grande richesse d'espèces. Similä *et al,* (2003) ont trouvé plus d'espèces de coléoptères spécialistes dans les zones les moins soumises à l'exploitation par rapport aux zones subissant une exploitation forte. Penttilä *et al,* (2004) ont étudié la richesse en espèces de champignons saproxyliques le long d'un gradient d'intensité d'exploitation forestière. Les zones les moins impactées par l'exploitation forestière possédaient un nombre d'espèces de champignons saproxyliques plus élevé que les zones les plus fortement exploitées.

De plus, les communautés de parasites d'organismes saproxyliques étaient absentes au sein des zones exploitées et n'étaient retrouvés que dans les zones non exploitées (Komonen *et al.,* 2000).

Au contraire, Müller *et al,* (2007), n'ont pas détecté un nombre d'espèces total de coléoptères, oiseaux ou mycètes différent entre les placettes exploitées et non exploitées. Cependant, la composition en espèces différait entre placettes exploitées et placettes non exploitées. Une proportion significativement plus importante d'espèces dépendantes des caractéristiques structurelles des OGF était présente au sein des placettes non exploitées.

De manière générale, on observe plus d'espèces dans les zones non exploitées que dans les zones exploitées, que ce soit pour les lichens, mousses, champignons, insectes, oiseaux ou chauves-souris. De plus, les espèces supplémentaires observées en zones non exploitées sont généralement des espèces spécialistes des phases finales du cycle sylvicole.

III.1.4.2) Espèces rares ou sur listes rouges

Les espèces généralistes sont capables de compenser la perte de leur habitat en s'installant dans des habitats de substitution de la même manière que dans leur habitat originel. Au contraire, les espèces spécialistes, dépendantes de conditions d'habitat singulières sont plus susceptibles d'être impactées par la disparition et fragmentation de leur habitat originel (Reunanen *et al.,* 2001). Parmi les espèces saproxyliques, certaines vont se spécialiser sur du bois fraichement mort, et d'autres sur de forts volumes de bois fortement dégradé. Ces dernières vont dépendre de niveaux trophiques supérieurs. Komonen *et al,* (2000) ont mis en évidence une simplification des niveaux trophiques d'habitat drastique entre zones exploitées et zones non exploitées. Les espèces dépendantes de hauts niveaux trophiques sont connues pour être particulièrement vulnérables à la diminution et à la fragmentation de leur habitat (Gibb *et al.,* 2008). Il en résulte la disparition de ces espèces des zones exploitées.

C'est par exemple le cas pour les polypores Penttilä *et al,* (2004), les mousses (Sabovljevic *et al.,* 2010 ; Odor *et al.,* 2006), les chauves-souris (Krusic *et al.,* 1996) ou les insectes (Grove, 2002a), en particulier les coléoptères (Siitonen et Saaristo, 2000). Cette diminution s'observe également sur plusieurs groupes au sein d'un même type forestier (Müller *et al.,* 2007). Les espèces prioritairement affectées par l'exploitation forestière sont celles dépendant des gros bois morts debout ou au sol (Odor *et al.,* 2006 ; Carlson, 2000 ; Roberge *et al.,* 2008 ; Virkkala *et al.,* 1993).

Les espèces rares peuvent donc être des espèces spécialistes, tributaires d'habitats prioritairement impactés par l'exploitation forestière. Elles sont de ce fait d'excellents indicateurs de l'état de conservation d'un milieu forestier. La rareté d'une espèce peut cependant être due à une répartition géographique restreinte, et non pas à un régime trophique élevé. Un indice de rareté des espèces de coléoptères saproxyliques a été proposé par Brustel, (2001) pour permettre d'évaluer l'état de conservation des forêts en France. Bien que ce travail ne comporte « que » 300 espèces, il est largement utilisé pour la sélection de zones d'implantation de réserves ou ilots de vieux bois en forêt. Un travail de synthèse et d'évaluation de la valeur patrimoniale des coléoptères saproxyliques de France est actuellement en cours (Bouget *et al.,* 2008).

IV) Quels outils pour la conservation des espèces saproxyliques ?

IV.1) Les réseaux d'habitat : Exemple de la Trame Verte et Bleue

La fragmentation des habitats est aujourd'hui considérée comme une des causes majeures de l'érosion de la biodiversité (Ehrlich, 1988 ; Wilcox et Murphy, 1985). Le risque d'extinction locale des espèces se maintenant sur de faibles surface est élevé (Gilg, 2004). Lorsque ces surfaces augmentent, leur fréquence augmente et leur probabilité d'extinction diminue (Sahlin et Schroeder, 2010). En réponse à ce phénomène, rétablir et/ou renforcer les liens entre les différentes parties d'un habitat en vue d'augmenter sa connectivité est une stratégie d'action. L'augmentation de la connectivité du milieu permet également d'augmenter virtuellement sa surface. C'est le principe du Réseau écologique paneuropéen (Conseil de l'Europe, 2003) et de la Trame Verte et Bleue (TVB), issue du Grenelle de l'Environnement.

IV.1.1) La sous-trame des très vieux bois (TTVB)

Le cas particulier du compartiment écologique des habitats favorables aux organismes saproxyliques permet de discerner une structure intrinsèque à la Trame Verte et Bleue, la **Trame de Très Vieux Bois** (TTVB). Elle est constituée d'éléments répartis sur l'ensemble du territoire national français, pouvant être forestiers ou non forestiers.

IV.1.2) Différents éléments constituant la TTVB

IV.1.2.1) Les éléments forestiers en forêt publique

Plusieurs mesures de gestion sont actuellement disponibles pour favoriser la conservation des cortèges saproxyliques forestiers en France (ONF, 2009 ; Mourey et Touroult, 2010) et vont constituer les éléments forestiers de la TTVB.

(i) Les réserves forestières sont des éléments clés pour la préservation de larges surfaces d'habitat. Le terme réserve traduit bien des réalités. En effet, le statut de protection et le degré d'intervention humaine autorisé ne sont pas les mêmes en fonction des pays et des dénominations (Parviainen *et al.,* 2000). Le principe d'action des réserves pour la conservation de la biodiversité repose sur le principe de la reconstitution naturelle des compartiments endommagés. Les zones forestières non soumises à exploitation vont alors petit à petit regagner des éléments caractéristiques des OGF (Gilg, 2004 ; Stockland *et al.,* 2012). Leur habitat reconstitué, les populations des espèces qui en dépendent vont alors pouvoir s'y développer de nouveau. Ceci traduit la nécessité d'avoir soit des populations relictuelles au sein de la forêt qui vont venir coloniser ces nouveaux habitats, soit de penser à l'échelle du territoire pour former un réseau fonctionnel permettant à des populations lointaines de venir coloniser ces nouveaux habitats. Pourtant, les réserves forestières sont plus généralement mises en place au niveau local qu'au niveau paysager (Schwartz, 1999).

(ii) Les ilots de vieux bois sont une mesure de conservation phare en France (ONF, 2009 ; Rouveyrol, 2009 ; Témoin, 2009 ; Tositti, 2004), mais aussi en Suisse (Lachat et Bütler, 2007), et au Canada (Déry et Leblanc, 2005). Il est à noter que des structures équivalentes existent dans les pays scandinaves (Timonen *et al.,* 2010) et en Amérique (Tittler *et al.,* 2001). Contrairement aux réserves forestières ils présentent l'avantage de pouvoir être mis en place sur de petites surfaces (1ha) et de ne pas présenter de grande perte de productivité. Parfois même, ils permettent d'obtenir des bois de grande qualité en fonction de leur nature. Le terme « Ilots de vieux bois » regroupe donc deux notions en France : les ilots de vieillissement et les ilots de sénescence.

L'ilot de vieillissement est un petit peuplement ayant dépassé les critères optimaux d'exploitabilité économique et qui bénéficie d'un cycle sylvicole prolongé pouvant aller jusqu'au double de ceux-ci. L'ilot de vieillissement peut faire l'objet d'interventions sylvicoles. Les arbres objectifs sont récoltés à leur maturité et, en tout état de cause, avant dépréciation économique de la bille de pied. (ONF, 2009). Les diamètres des arbres au sein des ilots de vieillissement seront donc plus importants qu'au sein des parcelles exploitées voisines. On s'attend alors à y trouver plus d'espèces, le diamètre des gros arbres étant un indicateur de la richesse du milieu (Grove, 2002b).

L'ilot de sénescence est un petit peuplement laissé en évolution libre sans intervention sylvicole et conservé jusqu'à son terme physique, c'est-à-dire jusqu'à l'effondrement des arbres (ONF, 2009). C'est une sorte de réserve forestière de toute petite surface.

En fonction de leur surface et de leur capacité à générer du bois mort, les ilots de sénescence peuvent être permanents ou itinérants (Lachat et Bütler, 2007). La taille moyenne d'un ilot de vieux bois est actuellement d'environ 1ha (Tositti, 2005), surface assurant la présence continue de bois mort au cours du temps (Lachat et Bütler, 2007). En fonction des contextes, la proportion objectif d'ilots de vieillissement peut aller de 2% à 5% ou plus (Tableau 1).

(iii) L'arbre-habitat est un élément qui vient renforcer le réseau créé par les réserves forestières et les ilots de vieux bois au sein de la forêt. Il s'agit généralement d'un arbre vivant porteur de dendromicrohabitats (cavités hautes, polypores, écorces déhiscentes…). Il peut également se

présenter sous la forme d'un vieil arbre ou d'un très gros arbre de l'essence objectif ou des essences d'accompagnement (ONF, 2009). Un cas particulier de l'arbre-habitat est l'arbre mort. Certains auteurs considèrent cet arbre comme du bois mort sur pied et ne l'intègrent pas en tant qu'arbre-habitat (Lachat et Bütler, 2007). Actuellement, l'ONF préconise le maintien d'une moyenne de 3 arbres-habitat par hectare, avec un minimum de 1 arbre mort à l'hectare (Tableau X) (ONF, 2009). Lachat et Bütler (2007) estiment pour leur part entre 8 et 12 le nombre minimal d'arbres-habitat à conserver par hectare dans les forêts Suisses pour qu'ils puissent assurer leur rôle de conservation et de relais. Ces arbres-habitat sont en effet supposés jouer le rôle de points de relais entre des habitats à plus grande échelle (ilots ou réserves forestières) (Lachat et Bütler, 2007).

<table>
<tr><th></th><th colspan="3">Surface forestière totale</th><th colspan="2">Cas particuliers</th></tr>
<tr><th></th><th>Moins de 300ha</th><th>300ha</th><th>Plus de 300 ha</th><th>Zones à forts enjeux de préservation</th><th>Zones de montagne</th></tr>
<tr><td>Ilot de vieillissement</td><td rowspan="2">Pas de seuil minimal</td><td rowspan="2">1%</td><td>2%</td><td>Entre 2% et 5%</td><td>De 2% à 5% ou plus</td></tr>
<tr><td>Ilot de sénescence</td><td>1%</td><td>Entre 1% et 3%</td><td>De 1% à 3% ou plus</td></tr>
<tr><td>Nombre d'aménagements pour arriver à l'objectif (ilots uniquement)</td><td>Pas de durée définie</td><td colspan="2">3 (entre 30 et 60 ans)</td><td colspan="2">3 ou moins (60 ans au plus)</td></tr>
<tr><td>Réserves forestières</td><td colspan="5">Pas d'objectif chiffré</td></tr>
<tr><td>Arbres-habitats (dont au moins un mort de plus de 35cm de diamètre)</td><td colspan="5">3 arbres habitats / Ha</td></tr>
</table>

Tableau 1 : Synthèse des surfaces et nombre d'éléments de la TTVB à conserver en forêts publiques. (ONF, 2009).

IV.1.2.2) Les éléments forestiers en forêt privée

La forêt privée représente environ 75% de la surface forestière Française (IGN, 2014). La mise en place des mesures conservatoires en faveur de la biodiversité est laissée à la discrétion des propriétaires privés. Ainsi, près de 75% de la forêt en France n'est pas soumise à des obligations de conservation. Ce constat est inquiétant. Les politiques publiques n'incitent pas les propriétaires privés à installer de telles structures en proposant des compensations financières (sauf dans le cas particulier des sites Natura 2000). Pourtant, la mise en place de mesures financières compensatoires serait bien perçue par les propriétaires privés, qui accepteraient alors l'arrêt d'exploitation local de leur forêt (Götmark *et al.,* 2000). La totalité des forêts privées en France n'est pas exploitée. Certains propriétaires ignorent qu'ils possèdent des territoires forestiers, et d'autres ne les exploitent pas. Ces zones sont alors assimilables à des réserves forestières intégrales passives, jouant un rôle déterminant dans la conservation de la biodiversité (Müller *et al.,* 2010).

IV.1.2.3) Les éléments non forestiers

La TTVB ne se limite pas aux structures forestières. Des éléments boisés tels que les parcs urbains ou encore les bosquets, les arbres isolés sont autant de constituants de la TTVB. Ils sont d'origine

variable (lambeaux d'anciennes forêts, arbres repères...) mais ont tous une valeur de refuge importante pour les espèces saproxyliques (Jonsell 2004 ; Ohsawa 2007 ; Vignon 2006).

Peu d'études se sont focalisées sur la capacité d'accueil des différents éléments non forestiers de la TTVB vis-à-vis des coléoptères saproxyliques. La plupart des études existantes à travers le monde concernent les fourmis (Gove *et al.,* 2009 ; Dunn, 2000), les chauves-souris (Lumsden et Bennett, 2005) ou encore les plantes épiphytes (Werner, 2011). En Europe, aucune étude n'a encore comparé la contribution respective de chaque élément non forestier de la TTVB vis-à-vis des coléoptères saproxyliques. Des études au cas par cas assimilables à des explorations faunistiques ont été menées pour certains de ces éléments (Carpaneto *et al.,* 2010 ; Dubois, 2009 ; Jonsell, 2004,2012 ; Ohsawa, 2007 ; Vignon, 2006).

La plupart de ces éléments sont en régression depuis 1960 (Boureau *et al.,* 2005 ; Pointereau et Coulon, 2006). Le rythme de disparition des haies était élevé entre 1960 et 1980 (45.000 km/an) puis a diminué entre 1980 et 1990 (15.000km/an) et s'est stabilisé depuis (Pointereau et Coulon, 2006). On observe également un accroissement de l'âge des arbres constitutifs des haies alors que leur linéaire diminue (Pointereau, 2001). Ceci pose la question de leur renouvellement et de la survie des espèces d'insectes saproxyliques qui s'y sont réfugiées.

V) Données d'étude

V.1) Données propres

Mes investigations de terrain se sont axées sur les chênaies de plaine du nord de la France, dans les contextes continentaux et atlantiques. En 2012, ce sont 11 sites forestiers qui ont été étudiés, et 5 sites forestiers avec leur pendant hors forêt en 2013. Dans tous les cas de figure, les peuplements étudiés étaient composés de très gros bois (DBH>70cm) à des densités variables.

V.2) Données mutualisées

En supplément aux données récoltées sur les sites d'étude exposés ci-dessus, nous avons pu travailler sur des jeux de données mutualisés entre différentes structures partenaires, nationales ou Européennes. Les types forestiers étudiés n'étaient pas limités à la chênaie mais comprenaient également des zones de hêtraie et de sapinière ainsi que des peuplements mixtes.

VI) Objectifs de recherche

VI.1) Les coléoptères saproxyliques en tant qu'indicateurs de la biodiversité saproxylique

La totalité des organismes saproxyliques en forêt est trop grande pour être appréhendée dans sa globalité. Nous avons choisi le groupe des coléoptères saproxyliques comme proxy d'étude à la totalité de la faune et flore saproxylique. Ce choix est basé sur le constat suivant : 30% des espèces forestières sont liées au bois mort et parmi elles, 30% sont des Mycètes et 20% des coléoptères (Stokland et Meyeke, 2008). Bien que le groupe des Mycètes soit plus représentatif de la totalité des organismes saproxyliques en forêt, l'échantillonnage de ce groupe ainsi que son identification sont délicates et nécessitent des compétences avancées. Les coléoptères saproxyliques sont en revanche fortement étudiés depuis quelques années, comme en témoigne l'abondante littérature scientifique

et naturaliste qui leur est dédiée à travers le monde. La possibilité de se reposer sur le réseau Entomologie de l'ONF pour les identifications de groupes particulièrement délicats a permis d'entériner ce choix. Mes compétences personnelles pour l'identification et l'intérêt porté au groupe d'étude (Annexe 1) sont venus soutenir ce choix.

VI.2) Axes de recherche

L'objectif de cette thèse est de mieux comprendre le rôle joué par les différents éléments de la TTVB à la conservation des espèces saproxyliques, aux échelles spatiales locales et paysagères. Cet objectif a été mené en déclinant notre approche en deux axes, correspondant aux deux échelles spatiales envisagées :

- **Quel est le rôle intrinsèque des éléments de la Trame de Très Vieux Bois à la conservation des coléoptères saproxyliques ?**

Nous cherchons à comprendre comment ces structures prises de manière individuelle vont contribuer à cette préservation. Nous avons étudié un élément particulier de la TTVB hors forêts, les arbres isolés. En forêt, nous avons étudié l'impact de la mise en réserve ou en ilot de vieillissement sur les caractéristiques structurelles du milieu –en particulier les compartiments « bois mort » et « dendromicrohabitats ». Ensuite, nous avons mis en relation modifications structurelles du milieu et caractéristique » des assemblages d'espèces échantillonnées (richesse spécifique, abondance, composition).

- **Quelle est l'influence de la quantité d'éléments de la TTVB dans le paysage sur les assemblages d'espèces de coléoptères saproxyliques ?**

Nous nous sommes focalisés sur l'importance de la quantité et qualité d'habitats favorables au niveau du paysage pour la conservation des coléoptères saproxyliques. Cette approche a été conduite en plaine et en montagne, au niveau national mais est également en cours d'étude au niveau Européen.

Indépendamment de ces problématiques principales, nous avons tenu à mieux comprendre les limites associées à notre groupe d'étude particulier, et les biais méthodologiques auxquels nous pourrions être confrontés. Nous avons donc commencé par mener une réflexion autour de la méthodologie d'échantillonnage des coléoptères saproxyliques et de l'influence de la quantité et qualité des données sur la qualité des résultats obtenus (Chapitre II).

Liste des travaux produits

Articles scientifiques

Chapitre	Papier	1er auteur	Statut	Année de publication	Titre	Revue	Terrain	Identification	Implémentation de la base de données	Rédaction	Analyses
II	1	Parmain	publié	2013	Influence of sampling effort on saproxylic beetle diversity assessment: implications for insect monitoring studies in European temperate forests	Agricultural and Forest entomology	-	5%	20%	80%	90%
	2	Parmain	publié	2014	Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests?	Bulletin of Entomological Research	0%	0%	800%	80%	90%
III	3	Parmain	en préparation	-	Extended rotations in French oak forests do not enhance saproxylic beetle diversity	-	95%	95%	100%	60%	100%
	4	Parmain	en préparation	-	Are solitary trees keystone structures for saproxylic biodiversity conservation?	-	100%	95%	100%	60%	100%
	5	Bouget	publié	2014	Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles?	Animal Conservation	-	<10%	10%	5%	90%
	6	Bouget	publié	2013	In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests	Biodiversity and Conservation	-	5%	10%	5%	0%
IV	7	Parmain	en préparation	-	Increasing the percentage of forest reserves in the landscape amplifies saproxylic beetle diversity both within and beyond reserve borders	-	-	<10%	10%	50%	90%
	8	Parmain	en projet	-	Are historical landscape characteristics drivers for actual sparoxylic beetle? Extinction debt effects at the European scale	-	20%	20%	80%	60%	Non évalué
Annexes	9	Rougerie	under review	2014	PASSIFOR: A reference library of DNA barcodes for French saproxylic beetles (Insecta, Coleoptera)	Biodiversity Data Journal	Sans objet	Sans objet	10%	2%	0%

Tableau 2 : Liste des publications académiques réalisées (ou en préparation) dans le cadre de la thèse. Le degré d'implication dans chacun des articles est estimé en pourcentage pour chaque tâche. La mention « sans objet » fait référence à un protocole particulier pour lequel ma participation a été de mettre à disposition le matériel biologique présent dans ma collection de références personnelle.

Conférences, colloques

Communications internationales :

Parmain, G., Bouget, C., (2014). Forest vs solitary Oak trees: Key habitats for saproxylic beetle conservation. *8th Symposium on the Conservation of Saproxylic Beetles*, Basel (Switzerland), 13-15 June 2014.

Communications nationales :

Parmain, G., Brin, A., Dufrêne, M., Bouget, C., (2012). Influence de l'effort d'échantillonnage sur l'évaluation de la diversité des coléoptères saproxyliques. *6e rencontres annuelles du Groupe des Entomologistes Forestiers Francophones (GEFF),* Epernay (51), 25-27/09/2012.

Bouget, C., **Parmain**, G., Gilg, O., Noblecourt, T., Nusillard, B., Paillet, Y., Pernot, C.,Larrieu, L., Gosselin, F., (2013). Influence de la durée de non exploitation sur la restauration des stocks de bois mort et micro-habitats et recolonisation par les coléoptères saproxyliques. *7e rencontres annuelles du Groupe des Entomologistes Forestiers Francophones (GEFF),* Brens (81), 21-24/09/2013.

Parmain, G., Bouget, C. (2014). Arbres solitaires: Eléments clefs pour la conservation de l'entomofaune saproxylique. *8e rencontres annuelles du Groupe des Entomologistes Forestiers Francophones (GEFF),* Lucelle (68), 16-18/09/2014.

Comptes-rendus d'échantillonnage

Compte-rendu d'échantillonnage:

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de Bercé (72), France, Sarthe*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 22 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de Bezange-la-Grande (54), France, Meurthe-et-Moselle*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 24 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière du Domaine de Candé (37), France, Indre-et-Loire*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 24 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de Lisle (55), France, Meuse*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 25 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de Loches (37), France, Indre-et-Loire*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 27 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale du MontDieu (08), France, Ardennes*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 19 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de Montgoger (37), France, Indre-et-Loire*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 22 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de Réno-Valdieu (61), France, Orne*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 20 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de Signy-l'Abbaye (08), France, Ardennes*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 20 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de Saint-Palais (18), France, Cher*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 26 p.

Parmain. G., Barnouin. T., Noblecourt. T., & Soldati. F., 2012. *Rapport d'échantillonnage de l'entomofaune forestière de la Forêt Domaniale de la Traconne (51), France, Marne*. Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2012, 21 p.

Parmain G., Barnouin T., Noblecourt T., & Soldati F., 2013. *Rapport d'échantillonnage de l'entomofaune des forêts de Marcenat, Souvigny et Yzeure et propriétés privées avoisinantes. France, Allier (03).* Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2013, 38 p.

Parmain G., Barnouin T., Noblecourt T., & Soldati F., 2013. *Rapport d'échantillonnage de l'entomofaune des Forêts Domaniales de Rambouillet et Marly-le-Roi et Domaines présidentiels associés. France, Yvelines (78).* Quillan: Office National des Forêts, Laboratoire National d'Entomologie Forestière. Décembre 2013, 30 p.

Organisation de la thèse

Cette thèse débute par une présentation des types de forêts étudiées, en particulier la chênaie (**Chapitre I**). La genèse de l'habitat 'forêt' ainsi que les enjeux économiques et de conservation associés y sont abordés.

Une réflexion autour des méthodologies d'échantillonnage des coléoptères saproxyliques employées est menée dans le **Chapitre II**. Cette partie vise à mieux comprendre les relations entre effort d'échantillonnage à l'aide de pièges d'interception et quantité de matériel collecté. Nous avons également mené une réflexion autour de la qualité des données générées par de tels échantillonnages, et l'impact que cela pouvait avoir sur les conclusions d'une étude. Cette approche est pour nous un prérequis à la réalisation des objectifs de cette thèse. Nous avons conduit une discussion propre à ce chapitre.

Publications associées à ce chapitre : Articles **1** et **2** (Tableau 2)

Le **Chapitre III** aborde l'étude des structures de la TTVB. A travers l'analyse de différents jeux de données mutualisées entre différents laboratoires et de deux jeux de données originaux créés aux cours de mes travaux, nous avons étudié l'effet concret des ilots de vieillissement, des réserves forestières et des arbres isolés extra-forestiers sur les assemblages de coléoptères saproxyliques. L'impact de chacun des éléments a été évalué au niveau local. Cette évaluation a été faite en deux temps : (i) évaluation des caractéristiques du milieu et (ii) impact du milieu sur les assemblages de coléoptères saproxyliques.

Publications associées à ce chapitre : Articles **3** ; **4** ; **5** et **6** (Tableau 2).

Le **Chapitre IV** vise à étudier les relations entre éléments de la TTVB et biodiversité des coléoptères saproxyliques à l'échelle paysagère. Nous avons étudié le cas particulier des réserves forestières à travers la mobilisation de deux importants jeux de données (GNB et RESINE). Un projet de co-analyse Franco-Tchèque y est décrit, et des éléments de matériels et méthodes sont proposés.

Publications associées à ce chapitre : Articles **7** et **8** (Tableau 2).

Enfin, l'ensemble des conclusions des études que nous avons menées ou auxquelles nous avons participé sont mises en perspective dans une discussion générale. Des éléments concrets de gestion sont proposés. Des pistes de futures recherches complémentaires à nos sont évoquées.

Chapitre I :

Modèles d’étude

Chapitre I : Modèles d'étude

I) Les forêts tempérées du Nord de la France

I.1) Dynamique naturelle

I.1.1) La genèse d'un habitat

Naturellement, une forêt se développe sur des étendues non boisées. Ce phénomène peut s'observer de nos jours en France par la déprise agricole. La surface forestière totale augmente (Cinotti, 1996). Des essences héliophiles vont coloniser ces espaces vides de forêts. En Europe, les essences pionnières sont principalement le saule, le peuplier, l'aulne et le bouleau (Rameau, 1999). Cette phase de colonisation est suivie du développement des essences pionnières, qui vont créer un couvert. Les espèces secondaires vont alors commencer à s'installer. Ces espèces ne tolérant pas les conditions de milieux ouverts sont dites sciaphiles. Ces essences ont de natures diverses en fonction des auteurs et de contextes considérés, mais sont principalement constituées par l'érable, le frêne, l'orme, le tilleul, le chêne, le merisier, le sorbier, le pin et le mélèze (Rameau, 1999). Une fois ces essences en place, le milieu va évoluer de manière cyclique au cours du temps. Cette évolution est nommée « cycle sylvigénétique ». Le développement naturel de la forêt est alors appelé sylvigenèse.

I.2) Les différents types de forêts explorées

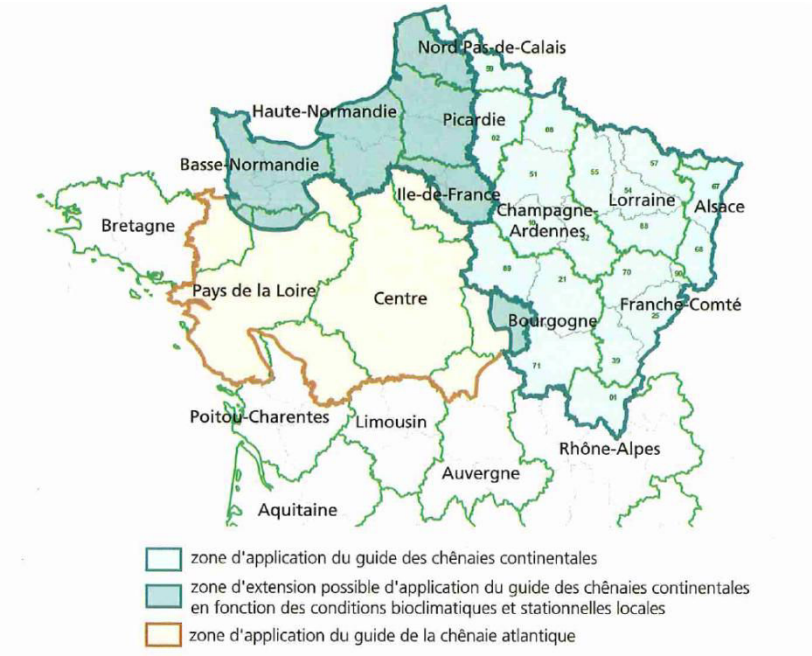
I.2.1) Cas particulier de la chênaie

Le cycle sylvigénétique tel qu'il est actuellement considéré ne permet pas l'apparition de forêts à peuplements dominants de chênes. En effet, le chêne ne fait pas parte des essences forestières dominantes des peuplements en phase optimale, mais est une essence post-pionnière / nomade (Rameau, 1999). Elle peut ainsi s'installer durant les phases de régénération et initiales, mais sera supplantée par d'autres espèces en phase optimale. C'est l'action de l'Homme sur la forêt qui a permis d'obtenir des peuplements dominants de chênes, en limitant la croissance des essences telles le hêtre, le tremble, ou le saule (Sardin, 2008). Vera (2000) a par ailleurs étudié des forêts de chêne et de hêtre réputées pour leur caractère mature et naturel en Europe (Fontainebleau, Bialowietza …) et a montré que la régénération naturelle des peuplements de chênaie n'avait pas lieu par opposition à celle du Hêtre. Taylor et Lorimer (2003) ont monté à partir de simulations que les forêts actuelles de chênes d'Amérique, si laissées en libre évolution, verraient leurs peuplements de chêne dominants disparaitre au profit d'autres essences. Le chêne n'y représenterait alors plus que 19% des arbres dominants du peuplement.

Il existe différents types de chênaie en France, chacune avec ces spécificités d'espèces et de traitement sylvicole.

I.2.1.1) Contextes bioclimatiques

La chênaie Atlantique s'étend de la région centre aux côtes atlantiques et a pour limite basse le département de l'Allier. La chênaie Continentale s'étend globalement de la Belgique à la région Centre (Carte 1). A elles deux, elles occupent grossièrement la moitié nord de la France. Les essences de chêne dominantes sont le chêne sessile et le chêne pédonculé. Le traitement principal appliqué à ces deux milieux est la futaie (Jaret, 2004 ; Sardin, 2008). La diversité des stations forestières et climatiques rencontrées sur ces deux paysages donne lieu à des recommandations de gestion adaptées au contexte local (Jaret, 2004 ; Sardin, 2008). Les diamètres d'exploitabilité des arbres de futaie sont fortement similaires, ainsi que le nombre de tiges objectifs à l'hectare.



Carte 1 : Répartition des chênaies atlantiques et continentales et limites d'application des guides sylvicultures relatifs (d'après Sardin, 2008).

La chênaie méditerranéenne comme son nom l'indique, s'étend sur tout le pourtour méditerranéen. Les essences de chêne dominantes sont le chêne vert, le chêne pubescent et le chêne liège, avec un traitement majoritairement en taillis (Maupeou, 1996).

I.2.1.2) Un milieu aux enjeux antagonistes

I.2.1.2.1) Economiques

La vente de bois est le secteur économique rapportant le plus de recettes à l'ONF (29.4% du total des recettes (ONF, 2013)). Le cours du bois fluctuant en fonction des années, il est primordial pour assurer la pérennité économique de conserver une production de bois de qualité, dont la valeur marchande ne va pas facilement diminuer. C'est le cas des chênes de fort diamètre à grain fin (Jaret, 2004). Ces derniers sont particulièrement recherchés par les tonneliers. Ainsi, des chênes issus de futaie avec des futs droits de plus de 10m de long, non vrillés peuvent se vendre à des tarifs dépassant la dizaine de milliers d'euros (Jaret, 2004).

I.2.1.2.2) Eclogiques (biodiversité)

Le chêne est l'essence ligneuse abritant la plus riche faune saproxylique d'Europe (Vodka *et al.,* 2009). Cette faune est principalement dépendante des arbres de fort diamètre, ou présentant des dendromicrohabitats. De plus, une proportion importante de ces espèces est considérée comme rares, et sont présentes sur les listes rouges de plusieurs pays (Procter et Harding, 2005 ; Nieto et Alexander, 2010). Certaines espèces sont également protégées au niveau Européen (*Osmoderma eremita* et *Cerambyx cerdo*, deux espèces spécialistes du genre *Quercus* (Nieto et Alexander, 2010)). En outre, les espèces associées aux hauts niveaux trophiques des dendromicrohabitats que peut supporter le chêne sont ponctuellement reconnues comme espèces parapluies. C'est par exemple le cas de *Limoniscus violaceus* (Gouix, 2011). Récemment, des espèces d'insectes nouvelles pour la science ont été découvertes en explorant les riches assemblages de coléoptères saproxyliques associés aux chênes (Buse *et al.,* 2013). Les enjeux de conservation de la diversité des espèces saproxyliques sont particulièrement forts pour le cortège associé aux chênes.

I.2.2) Autres contextes forestiers explorés

Bien que nous nous soyons fortement concentrés sur la chênaie et la biodiversité saproxylique associée, nous avons également étudié d'autres types forestiers, car ils sont aussi porteurs d'une biodiversité unique. La hêtraie en Europe est un milieu forestier largement étudié, en particulier pour sa qualité en tant que milieu d'accueil pour la biodiversité (Christensen *et al.,* 2005 ; Vandekerkhove *et al.,* 2009 ; Müller *et al.,* 2007, Meyer et Schmitt, 2011 ; Odor *et al.,* 2006). Les propriétés intrinsèques au bois de hêtre par rapport au bois de chêne assurent également une rapide mise à disposition des différents compartiments « bois morts » et « dendromicrohabitats ». L'avantage qui est procuré par cette rapide mise à disposition est contrebalancé par la rapide disparition de ces habitats, faiblement pérennes. L'intérêt de l'étude de la hêtraie à l'égard de la biodiversité saproxylique vient également de la répartition géographique et altitudinale du Hêtre. Celui-ci peut être présent en forêt de plaine comme en forêt de montagne, et est distribué sur une vaste partie du territoire Européen. Il est généralement associé au chêne en forêt de plaine, et au sapin en forêt de montagne. Les processus régissant la réponse de la biodiversité pourraient ne pas être les mêmes en plaine et en montagne. Ceci pourrait être dû aux différences de climat associées à chaque milieu, mais également à la différence d'intensité d'exploitation subie par ces milieux. En effet, bien que les zones de montagne aient été fortement exploitées, il a subsisté des zones trop pentues ou difficiles d'accès pour que l'exploitation soit aussi forte qu'en plaine. Partant de ce constat, nous nous sommes également intéressés aux peuplements de montagne, en particulier des peuplements de sapin en mélange (ou pas) avec du hêtre. La sapinière est reconnue en France pour héberger des espèces à très grande valeur patrimoniale, *i.e.* à très forts enjeux de conservation (Brustel, 2001).

Chapitre II :

Développements méthodologiques

Chapitre II : Développements méthodologiques

Publications associées à ce chapitre : Articles **1** et **2** (cf Tableau 2)

Partie I : Un besoin de maitrise des outils

I) Méthode d'échantillonnage

L'étude des communautés d'insectes saproxyliques représente un véritable défi pour le scientifique. Ces espèces sont généralement de petite taille, et ont des mœurs cryptiques (Nageleisen et Bouget, 2009). Elles sont particulièrement difficiles à contacter en prospection manuelle qui implique dans de nombreux cas l'altération ponctuelle de leur habitat. Pour pallier ces inconvénients, des méthodes de piégeage automatiques ont été mises en place. Il en existe un grand nombre, toutes avec leurs avantages et inconvénients (Leather, 2005). L'efficacité de plusieurs de ces dispositifs à contacter un grand nombre d'espèces de coléoptères saproxyliques du milieu a été comparée (Brustel, 2001 ; Nageleisen et Bouget, 2009). Ces méthodes sont complémentaires, elles ne contactent pas les mêmes espèces. Il faudrait donc idéalement combiner les différentes techniques d'échantillonnage sur un même site pour que la communauté échantillonnée soit la plus représentative possible de la communauté présente. La comparaison de l'efficacité et du coût des différentes méthodes entre elles ont été menées par divers auteurs (voir Brustel, 2001 ; Nageleisen et Bouget, 2009 pour des synthèses sur le sujet). Le ratio entre efficacité, coût et facilité de mise en œuvre sur le terrain ont permis de désigner le piège à interception multidirectionnel comme le meilleur compromis entre les différentes méthodes disponibles pour l'échantillonnage des coléoptères saproxyliques (Nagelaisen et Bouget, 2009). Ce dispositif est utilisé en France (Bouget *et al.,* 2009) mais également en Europe (Müller *et al.,* 2008 ; Stenbacka *et al,* 2010) et ailleurs dans le monde (Lamarre *et al.,* 2012 ; Grove, 2002b).

II) Effort d'échantillonnage

La capacité du piège à interception à échantillonner les coléoptères saproxyliques a fait ses preuves. L'augmentation de la quantité d'espèces contactées (dans le but d'inventaires ou d'études comparatives) peut se faire par deux moyens simples : la réplication spatiale des pièges (on augmente le nombre de pièges mis en place) ou la réplication temporelle (on augmente le nombre d'années sur lequel est conduit l'expérimentation). Contacter une majeure partie des espèces du milieu permet de généraliser les résultats à l'ensemble de la communauté.

III) Qualité des données

L'effort d'échantillonnage produit est variable et dépend des moyens humains et financiers disponibles. Ainsi, la quantité de données obtenue en fonction des études va dépendre de l'effort d'échantillonnage produit. La quantité de données influence la qualité des résultats obtenus. Chen *et al,* (2003) ont par exemple montré que des estimateurs de richesse basés sur une quantité de

données trop faible n'étaient pas pertinents. Cela amène à la mise en place de mesures de gestion peu efficaces voire totalement inappropriées.

III.1) Résolution taxinomique

Les coléoptères saproxyliques représentent environ 25% des espèces forestières. En terme concrets, cela représente environ 2500 espèces en France (Bouget *et al.,* 2008 ; Brustel, 2001). Ce chiffre, bien qu'impressionnant au regard du nombre d'espèces d'oiseaux en Europe et Afrique du nord réunies ('seulement' 900 espèces (Svensson *et al.,* 2014)) ne représente qu'une infime partie des espèces des coléoptères français, actuellement estimé à 11600 espèces (ARE, 2014). Les compétences requises pour identifier un tel nombre d'espèces ne peuvent être acquises qu'à travers plusieurs personnes et au cours de nombreuses années de pratique (ARE, 2014). Ces espèces sont réparties au sein de nombreuses familles, et ne sont pas toutes étudiées avec la même ferveur par les entomologistes. Ainsi, certaines familles sont délaissées, et relativement méconnues. Ces familles sont généralement exclues des jeux de données, car trop couteuses à identifier en temps et en moyens (Sebek *et al.,* 2012). Des méthodes ont été proposées pour réduire le temps alloué à la partie d'identification des espèces, en réduisant le niveau de résolution taxinomique ou en n'étudiant que des sous assemblages particuliers (Sebek *et al.,* 2012). L'impact que cela peut avoir sur les résultats d'études est inconnu.

IV) Quels développements particuliers ?

L'objectif de cette partie d'exploration méthodologique est de mieux comprendre les limites inhérentes à l'utilisation du piège à interception multidirectionnel pour l'échantillonnage des coléoptères saproxyliques et de l'impact que ces limites peuvent avoir sur les résultats d'études basés sur l'utilisation d'un tel dispositif.

- **Quel est l'effet de la réplication spatiale et/ou temporelle du dispositif d'échantillonnage sur la quantité d'espèces contactées, et l'impact sur les conclusions d'études ?**

Nous cherchons ici à avoir des éléments concrets permettant d'estimer les stratégies les plus efficaces pour l'augmentation de la quantité de données récoltées, avec un minimum de coûts. L'impact de la faible quantité de données sur les conclusions d'une étude est également étudié.

- **Quel est l'impact de l'exclusion ou de l'inclusion d'une famille dominante parmi les coléoptères saproxyliques sur les conclusions d'études ?**

L'exclusion des familles peu connues au sein des jeux de donnés de coléoptères saproxyliques est un processus permettant d'économiser du temps et des moyens. Nous cherchons ici à savoir quel est l'impact d'une telle mesure à travers l'utilisation d'un exemple concret.

Agricultural and Forest Entomology (2013), **15**, 135–145 DOI: 10.1111/afe.12008

Article1: Influence of sampling effort on saproxylic beetle diversity assessment: implications for insect monitoring studies in European temperate forests

Guilhem Parmain ⁎†‡, Marc Dufrene^ §¶, Antoine Brin ⁎⁎ and Christophe Bouget‡
⁎National Laboratory o f Forest Entomology, N ational Forest Office (ONF), 2 rue C harles P éguy, F-11500 Quillan, France, †Natural Patrimony Department, National Museum of Natural History, 36 rue Geoffroy St Hilaire, CP 41 75 231 Paris Cedex 05, France, ‡'Forest Ecosystems' Research Unit, National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), Domaine des Barres, F-45290 Nogent-sur-Vernisson, France, §Department of Natural and Rural Environnement Monitoring (SPW/DGARNE/DEMNA), Avenue Maréchal Juin 23, B-5030 Gembloux, Belgium, ¶Liege University, Gembloux Agro Bio Tech (GxABT) Forests, Nature, Landscape Department Passage des Déportés, 2, B 5030 Gembloux, Belgium, and ⁎⁎Purpan Engineering School, University of Toulouse, UMR INPT/INRA 1201 Dynafor, 75 voie du T.O.E.C., BP 57611, F-31076, Toulouse Cedex 03, France

Abstract

1 Saproxylic beetle diversity monitoring provides a tool for estimating the efficiency of forest conservation measures. Flight interception traps are commonly employed to monitor beetle assemblages, although little explicit knowledge of the efficiency of this trapping method is available. 2 The present study investigated how slight changes in sampling effort can influence species richness and species composition of assemblages in data sets from standard window-flight traps. 3 At both trap and plot levels, an additional year or an additional trap provided a 50% increase in the number of species detected (a 75% increase for rare species) and resulted in a different estimated composition of the assemblages. Adding 2 or 3 years of sampling gave twice as many species and resulted in assemblages that were 50% dissimilar. Increases in the detection of species and the dissimilarity of assemblages were similarly affected along a gradient of forest conditions, suggesting that changes in sampling effort were not affected by forest condition. 4 At the forest level, year or trap replication provided smaller increases in species richness (31% and 25%, respectively). Within sites, distance measures in species composition between traps did not differ significantly when based on 1 or 2 years of data. Using two traps per plot compared with one trap influenced comparisons between stand types, based on species richness, in 25% of the cases. 5 Species detection was similarly increased by either year replication or trap replication. The results of the present study highlight the significant role played by fine scale patterns of habitat structure and inter-annual variation with respect to determining catch size and assemblages of saproxylic species.

Keywords Biodiversity, dissimilarity, flight-interception trap, replication, species richness.

Introduction

Saproxylic organisms, comprising a functional group that depends on dead or dying wood (Alexander, 2008), have been used in Europe (as indicators of forest biodiversity (Nieto & Alexander, 2010) ever since the preservation of forest biodiversity associated with dead wood was recommended by the European Council in 1988 (Comite des Ministres,´ 1988a, b). They are also used

as a tool for estimating the efficiency of forest conservation measures in several countries around the world (Grove, 2002b; Hammond *et al*., 2004; Lachat *et al*., 2006; Ohsawa, 2007). Approximately 30% of European species that depend on forest habitats need dead wood to some extent (Stokland *et al*., 2004). Globally, the saproxylic biota is species rich (Grove, 2002a), although many species are threatened by loss and fragmentation of habitats with sufficient dead wood and veteran trees. Beetles account for a large proportion of saproxylic biodiversity [e.g. approximately 25% of the saproxylic species in Scandinavia (Stokland *et al*., 2004), second to fungi]. Foresters and conservationists are paying more attention to them than to saproxylic fungi or Diptera for both practical and ecological reasons. Many beetle species have high conservation value; 11% of species are considered as threatened at the European level (Nieto & Alexander, 2010) and they are assumed to provide valuable information on the quality and continuity of woodland habitats (Grove, 2002b). If saproxylic beetle diversity is to be used effectively as a management tool in forestry, more explicit knowledge about the efficiency of trapping strategies is needed. A sound beetle sampling strategy should focus on: (i) the choice of an efficient and standardized method, (ii) the timing of samples; and (iii) the spatial framework. Regarding the first point, window (flight interception) traps are widely employed for catching active flying saproxylic beetles (Økland, 1996; Wikars *et al*., 2005; Alinvi *et al*., 2006) because they are easy to replicate and standardize, and are assumed to represent local saproxylic beetle communities that could only be obtained with much more effort using active or extraction methods such as bark peeling, dead wood beating and emergence trapping (Siitonen, 1994; Økland, 1996; McIntosh *et al*., 2001; Alinvi *et al*., 2006; Hyvarinen *et al*., 2006). In most studies of saproxylic beetles, species richness (SR) estimates are commonly compared based on data from only on a single trapping year, although little is known about the errors involved. Martikainen and Kouki (2003) emphasized the importance of having large sample sizes (more than 200 species) when studying threatened species. Larger samples can be obtained by increasing the number of traps, by sampling for several years or by combining these two approaches. Using a variety of existing data from entomological surveys based on multiple-trap plots in France and Belgium, we assessed the variation in species richness and species composition (evaluated in terms of Sorensen dissimilarity) of the saproxylic beetle assemblages caught with standard window traps (Brustel, 2004) when traps or years of sampling were added. The available data were limited in range (3 years, two traps per plot at most), although they covered a wide range of forest conditions. The present study aimed to determine:

• How does an increase in local sampling effort (increasing the number of traps or yearly replication per plot) affect the assessment of species richness and assemblage composition at the trap, plot and forest level?

• Does the influence of sampling effort on the quality of biodiversity data vary with forest conditions?

• What are the contributions of trap replication exclusively, year replication exclusively and the combination of trap and year replication to variation in estimates of specie richness?

• Does an increased local sampling effort affect the results of ecological comparisons between stand types at the forest level?

Materials and methods

The window trap dataset

In the present study, we used datasets compiled using saproxylic beetles obtained from several biodiversity surveys and ecological studies carried out from 1999 to 2010 by different French organizations National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), National Forest Office (ONF), University of Toulouse-Purpan Engineering School (EIP), Office for Insects and their Environment (OPIE)] and DEMNA (Departement of Natural and Rural Environnement Monitoring) in Belgium. We only compiled data originating from unbaited or ethanol baited (methylated spirit, 20%) window traps, suspended approximately 1.5 m above the ground. The trap was the basic sampling unit; at most, two traps, located approximately 20–60 m apart, were grouped to represent captures from the same plot (i.e. the same forest stand). Plots were grouped in sites, which were forests or a cluster of close forests dedicated to the same research project. When several trapping years were available for a given plot, we included only data from consecutive years. We divided the overall dataset into three subsets to analyze the effects of replication on saproxylic beetle diversity assessments (species richness and assemblage composition) after aggregating the data at three spatial scales (trap, plot and forest): (i) the Multi-Year-Trap set (MYT) at the trap level, to study the effects of year replication (one trap sampled over several years), (ii) the Multi-Trap-Plot set (MTP) at the plot level, to study the effects of trap replication (two traps; i.e. one additional trap located near the first, and sampled one single year) and (iii) the Multi-Trap-Multi-Year-Plot set (MTMYP), at the trap and plot levels, to compare the relative effects of trap and year replications. We also analyzed the consistency of the effects of trap or year replication over spatial scales, by upscaling from the trap/plot to the forest level on selected well-replicated sites. In the MYT subset, we selected sites in which plots had been sampled at the same place for two or three consecutive years. The MYT dataset contained 72 plots, for a total of 299 traps in 19 sites (Table 1). Six sites (*n* traps ≥ 10), with 239 traps in 50 plots were selected for analyses at the forest level (at least 10 traps cumulated over the same forest; Table 2). In the second data subset (MTP), a basic plot consisted of two replicate traps, separated by about 20 m (Bouget & Brustel, 2009) or 60 m (in the ORLEANS and BELGWAL datasets). The MTP dataset included 14 sites for 294 plots and 588 traps (Table 1). Eight sites (*n* traps ≥ 10), with 257 plots and 514 traps, were selected for analyses at the forest level (Table 3). In the BELGWAL set, we considered only the first two traps in each plot, although the data provided by one of them during the second sampling year were analyzed as a new replicate. An independent analysis of trap replication from one to eight traps using the Belgian set only would be too idiosyncratic, and weakened by the small sample size (22 plots only). At the multiple-plot forest level, we also studied whether trap replication influenced the significance, magnitude and direction of the faunistic differences between stand types. Environmental variables describing the stand type and required to answer a transversal ecological question (e.g. dead wood poor versus dead wood rich) were available on eight sites only in the MTP set. We used these eight sites to compare managed versus unmanaged stands (Auberive, Fontainebleau), dead wood-poor versus dead wood-rich stands (Rambouillet, BelgWal Year1, BelgWal Year2, Landes) and overmature versus mature stands (Tronc¸ais-CEM, Coppices). In the third data subset (MTMYP), we selected two-trap 2- year plots from the MYT dataset. We excluded the third year for some sites because a third trap per plot was not available (exept for BELGWAL). This set (i.e. MTMYP) included 16 sites, 36 plots and 72 traps

(Table 1). Samples available for this analysis were well distributed over the ecological forest gradients.

Environmental data

Three environmental factors and one methodological factor were used to describe trap features. The environmental variables qualifying trap location were: forest type (three levels: 'conifer', 'deciduous' and 'mixed'), altitudinal group (two levels: 'highland' and 'lowland', with the reference altitude distinguishing the levels being 1000 m above the sea level) and climatic (or biogeographical) domain [four levels according to the ETCB (European Topic Centre on Biological Diversity) (2006): 'alpine', 'atlantic', 'continental', 'continentalMediterranean']. Data from alpine or Mediterranean regions were insufficient to provide rigorous tests. The use of bait in the trap (methylated spirit, 20%) was the only methodological factor considered (two levels: 'ethanol-baited' and 'unbaited'; Table 3).

Beetle data

The beetle records from different sets first had to be harmonized, both with respect to nomenclature and saproxylic status. We choosed to follow the French database FRISBEE developed by Bouget *et al*. (2008). Only those records from families for which beetles were identified to the species level were used for the present analysis. These included Alleculidae; Anobiidae; Anthribidae; Biphyllidae; Bostrichidae; Bothrideridae; Buprestidae; Cerambycidae; Cerophytidae; Cerylonidae; Ciidae; Cleridae; Cucujidae; Curculionidae (Scolytinae only); Elateridae; Endomychidae; Erotylidae; Eucnemidae; Histeridae; Laemophloeidae; Leiodidae; Lucanidae; Lycidae; Lymexylidae; Melandryidae; Monotomidae; Mycetophagidae; Nitidulidae; Nosodendridae; Oedemeridae; Phloeostichidae; Prostomidae; Pyrochroidae; Salpingidae; Scarabaeidae; Silvanidae; Sphindidae; Tenebrionidae; Tetratomidae; Trogidae; Trogossitidae; Zopheridae. Several beetle families not studied in a majority of the sets were excluded from our analyses: Aderidae, Alexiidae, Cantharidae, Clambidae, Corylophidae, Cryptophagidae, Dasytidae, Dermestidae, Eucinetidae, Latridiidae, Mordellidae, Ptiliidae, Scirtidae, Scraptiidae, Scydmaenidae, Sphaeritidae, Staphylinidae and Throscidae. A total of 643 saproxylic beetle species [507 common species (79%) and 136 rare species (21%)] were present in the studied datas. They belonged to 42 families (or sub-families). We characterized each species with conservation value (at the country level) either as 'common' (IP = 1 or 2) or 'rare' species (IP = 3 or 4), in accordance with principles discussed by Brustel (2001) and the database FRISBEE (Bouget *et al*., 2008). In this database, each species has a patrimoniality index (i.e. conservation value; IP), in other words its degree of geographical rarity in France, with four levels: (i) common and widely distributed species; (ii) not abundant but widely distributed species, or only locally abundant species; (iii) not abundant and only locally distributed species; and (iv) very rare species (known in less than five localities or in a single 'county' in France). The 'all species' group contains both the 'common' and the 'rare' species.

Statistical analysis

Because the abundance of beetles was not always available, we only considered beetle occurrence for our analyses.We calculated two major indices based strictly on presence-absence data: (i) the mean benefit of SR (SR-Benefit) and (ii) the mean assemblage dissimilarity between traps or years. We defined the SR-Benefit as the percentage increase in species added by a second trap or

year, as follows: General formula: SR-Benefit = *(*SR*(*1+2*)*-SRi*)* Sri × 100 (1) with *i* = year 1 or 2 (MYT subset), or trap 1 or 2 (MTP subset). Mean percentages were calculated over plots, forests or years, depending on the comparison. Mean assemblage dissimilarity was used to interpret thesignificance of the additional captures for understanding the assemblages.The assemblage dissimilarity between plots or years was calculated as the Jaccard–Dice–Sorensen index (Oksanen *et al*., 2011). To test the influence of environmental characteristics and the use of bait in the traps on the species richness benefit, we fit generalized linear mixed models (GLMER) (Bolker *et al*., 2009), assuming a binomial distribution, with site and plot as random factors and including an observation-specific random intercept to account for possible overdispersion (Elston *et al*., 2001).We tested the significance of effects by comparing factorial models and a null model with a likelihood ratio test (LRT). A Tukey's multiple-comparison test was performed to identify where the differences occurred. We set the significant value of the LRT at 0.01% to limit type II errors. In the MYT within-site between-trap level analyses, we tested the effects of different combinations of 1, 2 and 3-year sampling designs on SR-Benefit and dissimilarity: a second sampling year after the first one (SR-Benefit A), a third sampling year after two first consecutive sampling years (SRBenefit B) and two additional sampling years after a single first one (SR-Benefit C). In the same way, the dissimilarity value was calculated among first-year and second-year or third-year samples. Dissimilarity analyses were always conducted with assemblages composed of all species; a potential more restricted analysis of rare species assemblages was not useful as a result of the small proportion of rare species in our data. The same testing strategy as that used for SR-Benefit was applied for dissimilarity. At the forest level, we only considered the first 2 years of sampling to calculate the difference in species richness between one and two sampling years (see general formula): with SR = Specific Richness and *y*(i) = year of sampling 1 or 2. We used Mantel tests (method = Spearman, 999 permutations) to test whether within-site between-trap distance matrices based, respectively, on 1- or 2-year data were correlated. We compared the effect of additional traps within sites in terms of SR-Benefit and dissimilarity values during single years between one- and two-trap plots [SR = Specific Richness; *t*(*n*) = trap number] [possible combinations for each plot: SR*t*1 ∼ SR*t*(1 + 2); SR*t*2 ∼ SR*t*(1 + 2)]. The effects of methodological and environmental factors were tested with a GLMER, assuming a Gaussian distribution with a log + 1 transformation of the raw data. The model was fit with site as a random factor. The dissimilarity value was computed between one-trap and two-trap plots. The same testing strategy as that used for SR-Benefit was applied for dissimilarity [see the general formula above, with SR = Specific Richness and *t*(i) = trap number 1 or 2]. We used Mantel statistics on one-trap or two-trap data to test whether the distance measures in species composition between traps (i.e. assemblage dissimilarity) was influenced by the number of traps per plot. To evaluate the contribution of each replication mode (trap or year) to total species richness, we partitioned the increase in richness observed in the MTMYP dataset into 'exclusive' (species contacted by one mode of replication only) and 'interactive' (species contacted by both modes of replication) effects of trap or year replication by a method adapted from Alatalo and Alatalo (1977). We used relativized calculations (i.e. the relative number of additional species compared with data from single traps and years). At the forest level, we compared species richness (only the 'all species' group) between two stand types A and B, estimated with one or two traps per plot. Species richness was assessed using the order-1 Chao richness estimator corrected for bias (Colwell, 1997) with 100 sample randomizations to calculate SD. The species richness difference was: Species richness difference = *(*RSB-RSA*)* RSA × 100 (2) with RSA and RSB being order-1 Chao estimators of the species richness in the A and B stand types, respectively. We observed whether the A-B dissimilarity values (± SD)

computed for onetrap or two-trap plots overlapped. All statistical analyses were conducted using estimateS (Colwell, 1997) and r (R Development Core Team, 2010) with the lme4 (Bates *et al*., 2011), mgcv (Wood, 2008), mvtnorm (Genz *et al*., 2011), multcomp (Hothorn *et al*., 2008) and vegan (Oksanen *et al*., 2011) packages.

Results

Effects o f year replication o n b eetle diversity assessmentsat trap and f orest levels

The MYT trap level dataset included 517 species [417 common species (81%) and 100 rare species (19%)]. At the trap level, adding a second year of sampling gave a mean SR-Benefit value of +53% (Fig. 1) and the mean dissimilarity of assemblages between paired 1-year and 2-year designs was 36% (Fig. 2). At the forest level, using a second year of sampling increased species richness by +31%. The mean Mantel correlation between the within-site distance matrices of 1- and 2-year data was nonetheless 65%, and significant in all cases studied. Within-site between-trap distance matrices based, respectively, on 1-year or 2-year data did not differ (Table 2). Including year-to-year variation led to notable increases in understanding of biodiversity. Overall, the number of species detected after 3 years of sampling was almost twice as large as the number of species after trapping only for 1 year (+88%) (Fig. 1). The 3-year assemblages were almost half as dissimilar as the 1-year assemblages (D = 47%; Fig. 2). At the trap level, adding a third year after 2 years of sampling provided only a mean SR-Benefit value of +27% (Fig. 1). Assemblages based on 3 years of data were only 20% dissimilar to those from 2 years of collecting. The SR-Benefit values for common species were similar to those calculated for the whole assemblage. However, these were much higher for the group of rare species only: +63% from a 1-year design to a 2-year design and even +112% from a 1-year design to a 3-year design (Fig. 1). Benefit values were much more variable for rare species only (the confidence interval was wider; Fig. 1). At the trap level, we did not observe any effect of forest type, climatic domain, altitudinal group or baiting status on of SR-Benefit or assemblage dissimilarity in any analysis.

Effects of trap replication on beetle diversity assessments at trap and forest levels

The MTP plot level dataset included 511 species [417 common species (82%) and 94 rare species (18%)]. Using two traps/plot provided a mean SR-Benefit value of +48% compared with using one trap/plot (Fig. 1). This value was similar for analysis of common species only (+46%) but was much higher for data about rare species (+78%). Mean assemblage dissimilarity between designs with paired one-trap and two-trap plots was 33% (Fig. 2). At the forest level, two-trap plots provided 25% more species, on average, than one-trap plots. Nonetheless, the mean Mantel correlation value between the within-site distance matrices of one- and two-trap plots was 66% and was consistently significant (Table 2). Similar to the analysis of MYTs, we did not find any relationship between SR-Benefit or assemblage dissimilarity that could be related to forest type, climatic domain or altitudinal group, or related to trap bait.

Comparative effects of trap and year replication on beetle diversity assessments at trap and forest levels

On average, sampling designs with two traps per plot or two sampling years returned more species and the effects of an additional trap or an additional year were similar (Fig. 3). The relative

increase in richness as a result of trap replication exclusively was approximately 48%, whereas the increase as a result of year replication exclusively was 53%. However, the increase reflected in both approaches to replication was much lower for common species (mean of 17%). These effects were caused mostly by additions of rare species in the catches (Fig. 3); the increase as a result of the addition of a single trap was 43.8% and the increase as a result of a second year of data was similar at approximately 44.7%. By contrast to the results reported above for common species, increases in rare species were more commonly seen in both kinds of replication (40.8%) (Fig. 3). The increase was explainable by trap replication exclusively, by year replication exclusively and by both replication modes redundantly. However, the relative increase in the number of rare species was highly variable.

Effect of trap replication on ecological comparisons of stand types

In all datasets, assemblages from the stand types compared (i.e. managed/unmanaged, dead wood poor/rich, mature/overmature) were less dissimilar with two traps (mean of 68%) compared with one trap per plot (73%); however, these dissimilarity values (± SD) always overlapped. On average, over the eight cases studied, the difference in species richness between the two stand types was similar using onetrap or two-trap plots (approximately 20% as absolute values in both cases). The magnitude of this difference between two- and one-trap plots depended on the case. No significant changes in the direction (A > B or B > A) of the difference between stand types was observed using one-trap or two-trap plots. However, in terms of estimated species richness, two comparisons gave significant A–B differences with two-trapplots only (Table 4). The only significant A–B difference found with one-trap plots remained significant using data from two-trap plots.

Discussion

Replication and species richness estimates

Adding both traps and years to studies of saproxylic beetle assemblages dramatically increased the number of beetle species collected at either the plot or forest level. On average, at the plot level, adding both an additional year and an additional trap provided a 50% increase in the number of detected species. The impact was more striking for rare species with a 75% increase in the number of species. On average, assemblages based on fewer traps and years were 35% dissimilar to those with more extensive samples. At the forest level, either year or trap replication provided a lesser increase in species richness (31% and 25%, respectively). Species detection was similarly increased by either year replication or trap replication (one to two traps). Despite large differences in species detection, ecological studies that ask functional questions about the general effects of various treatments or management strategies may not be deeply affected, although the magnitude of differences may be considerably underestimated. However, the problem remains for those who aim to monitor biodiversity as a conservation measure. They are limited by the efficiency of sampling schemes and the extent to which possible approaches provide sufficient data (especially on rare species).

Temporal consistency and yearly variations

Our results support the findings of White *et al*. (2006) concerning the importance of considering the yearly variation in species assemblages when estimating species richness and

assemblage characteristics. Increases in species number or contrasts in assemblage composition were driven more by rare than by common species. Similarly, Martikainen and Kaila (2004) showed that rare species richness varies greatly between years and does not vary synchronously among forests. During a 10-year study, they observed a low between-year dissimilarity for common species (approximately 20–30%) but a higher between-year dissimilarity for rare species. They showed that most of the common species observed over a 10-year sampling period had already been sampled in the first 3 years. In the present study, successively adding a second or a third sampling year (compared with 1 year only) gave 50% dissimilar assemblages, twice the number of species and 112% more rare species at the trap level. Even at the forest level, a 1-year replication provided a 31% increase in species richness. Inter-annual variation of saproxylic beetle assemblages is driven by several processes: beetle density and flight activity (Nageleisen & Bouget, 2009), meteorological variations (Williams, 1940; Rink & Sinsch, 2007), multi-year developmental cycles, variation in mean reproductive activity and the proportion of reproducing individuals driven by food availability and/or weather factors, and, finally, yearly variations in predator effects on prey populations (Turchin *et al*., 1999). These sources of variation are well appreciated for ground beetles (Klenner, 1989; Niemela *et al*., 1992; Heyborne *et al*., 2003; Irmler, 2003; Scott & Anderson, 2003) and also for saproxylic beetles (Ranius, 2001; Martikainen & Kouki, 2003). These variations lead to a 'time-dependent species accumulation'. A multiple-year sampling strategy reduces the influence of between-year variations on data quality (Martikainen & Kaila, 2004).

Between-trap within-plot variations

Small-scale variation in microclimatic conditions, habitat and microhabitat distribution patterns among plots may lead to between-trap variation in beetle catches. The influence of small-scale heterogeneity in beetle habitats on trap catches has already been shown in pitfall trap data for carabid beetles (Niemela *et al*., 1986; Desender & Pollet, 1988; Niemela & Spence, 1994; Brose, 2002). The importance of the immediate surroundings on catches of freely hanging flight intercept traps has also been demonstrated (Sverdrup-Thygeson & Birkemoe, 2008). Our data showed significant assemblage dissimilarity between catches of two traps located only approximately 20 m apart in the same stand. The results obtained in the present study therefore strengthen the hypothesis that finescale patterns of habitat structure could play an important role in trap catches. Although traps may be located close together, data will differ depending on whether or not they are in flight corridors, near rich microhabitats, or in open or closed spots. At a larger spatial scale (i.e. a forest), the SR-Benefit associated with trap replication appears to decrease; its value at the forest level is halved compared with the value at the local plot level (site = 25%; plot= 50%). Nonetheless, the results of research projects at the forest level may be affected to some extent by trap replication. For example, trap replication strengthened some previously insignificant trends in the present study. Simply doubling the number traps per plot changed the results for ecological comparisons of species richness in 25% of the cases studied. However, the comparison of assemblages in the selected stand types did not differ significantly among one-trap or two-trap plots.

Sampling rare species

Sampling rare species is especially challenging because they represent only a small part of the total number of species caught (McArdle, 1990), approximately 20% in our data. Unlike some studies (Niemela *et al*., 1990; Novotny & Basset, 2000; Grove, 2002b) that define rare species as

those poorly represented in their samples, we followed Martikainen and Kaila (2004) and *a priori* defined as rare those species listed as such in reliable databases (i.e. the French FRISBEE database in our case; Bouget *et al*., 2008). For the results obtained in the present study, at the plot level, all SR-Benefits associated with year replication were significantly higher for rare than for common species. Moreover, the annual SR-Benefit remained high (+73% of rare species from 1- to 2-year replicates, +38% of rare species from 2- to 3-year replicates) throughout a 3-year sampling period. Furthermore, Martikainen and Kaila (2004) demonstrated that the annual number of detected rare species is constant throughout a 10-year sampling period. A multi-year study would therefore be particularly valuable to detect a large amount of rare species. Martikainen and Kouki (2003) and Martikainen and Kaila (2004) observed that catches of rare species in small samples are random and that between-site comparisons based on such limited data do not provide very useful results. In the present study, year or trap replication provided an equivalent +75% increase in the number of detected rare species at the plot level. Hedgren and Weslien (2008) showed that selective trap placement (near well-known rich microhabitats) was a more efficient way of catching rare species than random trap placement. In the data obtained in the present study, even if adding a second trap per plot is assumed to sample a wider range of microhabitats at the plot scale, the relative and net increase in rare species detection with an additional trap was not higher than that with an additional sampling year. Data from a second sampling year accounts for between-year variation in rare beetle species density and activity.

Practical recommendations for saproxylic beetle diversity surveys

Given the high between-trap variation in species number and composition within plots, we recommend that ecological comparisons in species richness should be made at the plot level and not at the trap level. Our efforts to partition the effects on increase in species richness suggest that an extra trap had a similar effect to an extra year. However, yearly replication will accommodate mainly inter-annual variation in species occurrences, and trap replication will probably accommodate microhabitat variation (Hedgren & Weslien, 2008). In our analysis, the additional species differed between spatial and temporal replication modes. For common species, the gross effect of sampling replication (both trap and year) was significantly lower than the trap or the year replication effect. In other words, the specific effect on catches of either yearly variation or smallscale habitat heterogeneity was stronger than a raw replication effect (whatever the mode). For rare species, however, the interactive effect of trap and year replication on the increase in species richness was as important as the exclusive effects of trap or year replication. As previously suggested by Martikainen and Kaila (2004), the raw effect of replication therefore appears to be more important for rare species. A complete comparison of relative benefits of these two replication approaches should take costs into account. On average, field work accounts for only 20% of the working time for data collection in a monitoring or research programme, whereas the remaining 80% is sorting and identification work in the laboratory (Bouget, 2009). However, this feature depends strongly on the spatial extent of the programme because field costs indeed grow higher as the spatial scale of programmes increases. Thus, trap replication is recommended in largescale programmes, mainly for economic reasons. The required sampling strategy should obviously take into account space and time constraints dependent on the objectives of the sampling programme (analysis of environment–biodiversity relationships, long-term monitoring, intensive inventory, etc.). Power analyses are needed to better define the minimum number of traps per plot required to be able to detect at least 5% differences between two groups of plots. Similarly, at the forest level, it would be useful to better understand the minimum number of plots required to compare two groups of sites. To detect most

common species in a site, Martikainen and Kaila (2004) suggested using at least 20 traps during one single year. Plots containing a larger number of traps are required to properly study the sample-dependent species accumulation rate.

Conclusions and perspectives

Our analyses were based on existing data obtained from France and Belgium after compiling them in a way that permitted comparison. Significant benefits of replication were demonstrated despite a narrow range of year or trap replication. Slight variation in sampling effort (adding trap or year) deeply affected the quality of data. Further studies about the relationships between samplingeffort and catch characteristics based on a broader range of raw data (longer time series, denser sampling plots) will be useful for suggesting practical guidelines with respect to the sampling strategies used in monitoring schemes. A longer time frame for studies explicitly designed to support this type of analysis would facilitate the better analysis of time-dependent species accumulation rates. In addition, long-term studies would allow us to better understand inter-annual fluctuations in assemblage composition (Kozlov *et al*., 2010) and the impacts of global patterns of increasing or decreasing populations (Conrad *et al*., 2004; Salama *et al*., 2007), especially under the influence of climate change. Unfortunately, long-term, large-scale intensive insect sampling designs are scarce despite their obvious relevance to effective biological conservation and efficient biodiversity monitoring. The collection of such data is currently limited by financial constraints, a lack of qualified personnel or by institutional changes in research orientations (Jackson & Fureder, 2006). We hope that the findings of the present study, aiming to better understand the sampling methods for saproxylic beetles, provide or improve existing tools and aid in the design of cost-effective biodiversity monitoring schemes.

Acknowledgements

We thank Frederic Gosselin for his help with the data analysis and for helpful comments on the first drafts of the paper; Pavel Sebek for his contribution to the data compiling; and Bruno Meriguet, Olivier Rose, Thomas Barnouin, Fabien Soldati, Herve Brustel, Thierry Noblecourt, Lionel Valladares, Benoit Nusillard and Carl Moliard for help with data collection. We are indebted to John Spence and two anonymous rewiers for their useful comments on an earlier version of the manuscript. We also thank Vicki Moore for checking and improving our written English.

References

Alatalo, R.V. & Alatalo, R.H. (1977) Components of diversity: multivariate analysis with interaction. *Ecology*, **5 8**, 900–906. Alexander, K. (2008) Tree biology and saproxylic coleoptera: issues of definitions and conservation language. *Revue d'Ecologie (Terre Vie)*, **63**, 1–7.

Alinvi, O., Ball, J.P., Danell, K., Hjalten, J. & Pettersson, R.B.´ (2006) Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. *Journal of Insect Conservation*, **11**, 99–112.

Bates, D., Maechler, M. & Bolker, B. (2011) *lme4: Linear Mixedeffects Models Using S4 Classes*. R package version 0.999375-39 [WWW document]. URL http://CRAN.R-project.org/package=lme4 [accessed on 1 February 2012].

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Bouget, C. (2009) Levels of taxonomic resolution in forest entomology studies: needs, contingencies and perspectives. *Mémoires de la Société Entomologique de France*, **8**, 75–80 (in French).

Bouget, C. & Brustel, H. (2009) Chapter 4: target insect groupes in temperate forests, II – Saproxylic Coleoptera. *Forest Insect Studies: Methods and Techniques. Key Considerations for Standardisation. An*, *Overview of the Reflections of the 'Entomological Forest Inventories' Working Group (Inv.Ent.For)*. *Vol. 19: Les Dossiers Forestiers* (ed. by L. M. Nageleisen and C. Bouget), pp. 100–111. Office National des Forets, France.

Bouget, C., Brustel, H. & Zagatti, P. (2008) The French information system on saproxylic beetle ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation status. *Revue d'Ecologie (suite de La Terre et la Vie)*, **10** (Suppl), 33–36 [WWW document]. URL http://frisbee. nogent.cemagref.fr/index.php/en [accessed on 1 February 2012].

Brose, U. (2002) Estimating species richness of pitfall catches by nonparametric estimators. *Pedobiologia*, **46**, 101–107.

Brustel, H. (2001) *Coléoptères saproxyliques et valeur biologique des forêts françaises*. PhD Dissertation, University of Toulouse, Institut National Polytechnique.

Brustel, H. (2004) 'PolytrapTM' a window flight trap for saproxylic beetles. *Third Symposium and Workshop on the Conservation of Saproxylic Beetles*, Lativa.

Colwell, R.K. (1997) *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 8. User's Guide and Application*. University of Connecticut, Storrs, Connecticut [WWW document]. URL http://viceroy.eeb.uconn.edu/EstimateS [accessed on 1 February 2012].

Comite des Ministres (1988a)´ *Recommandation N◦ R (88) 10 du Comité des Ministres aux états membres pour la conservation des organismes saproxyliques et leurs biotopes (adoptée par le Comité des Ministres le 13 juin 1988, lors de la 418e réunion des Délégués des Ministres)*. Comite des Ministres (1988b)´ *Recommandation N◦ R (88) 11 du Comité des Ministres aux états membres pour la conservation des organismes saproxyliques et leurs biotopes (adoptée par le Comité des Ministres le 13 juin 1988 lors de la 418e réunion des Délégués des Ministres)*.

Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R. & Warren, M.S. (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation*, **8**, 119–136.

Desender, K. & Pollet, M. (1988) Sampling pasture carabids with pitfalls: evaluation of species richness and precision. *Mededelingen van de Faculteit Landbouwwetenschappen van de Rijksuniversiteit Gent*, **53**, 1109–1117.

Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C. & Lambin, X. (2001) Analysis of aggregation, a worked example: numbers of ticks on red grouse chick. *Parasitology*, **122**, 563–569.

ETCB (European Topic Centre on Biological Diversity) (2006) *The Indicative Map of European Biogeographical Regions: Methodology and Development*. Museum National d'Histoire Naturelle, France.

Genz, A., Bretz, F., Miwa, T., Mi, X., Leisch, F., Scheipl, F. & Hothorn, T. (2011) *mvtnorm: Multivariate Normal and t Distributions*. R Package Version 0.9-96 [WWW document]. URL http://CRAN.Rproject.org/package=mvtnorm [accessed on 1 February 2012].

Grove, S.J. (2002a) Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, **33**, 1–23.

Grove, S.J. (2002b) The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biological Conservation*, **104**, 149–171.

Hammond, J.H.E., Langor, D.W. & Spence, J.R. (2004) Saproxylic beetles (Coleoptera) using Populus in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. *Canadian Journal of Forest Research*, **34**, 1–19.

Hedgren, O. & Weslien, J. (2008) Detecting rare species with random or subjective sampling: a case study of red-listed saproxylic beetles in boreal Sweden. *Conservation Biology*, **22**, 212–215.

Heyborne, W.H., Miller, J.C. & Parsons, G.L. (2003) Ground dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA. *Forest Ecology and Management*, **179**, 123–134.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.

Hyvarinen, E., Kouki, J. & Martikainen, P. (2006) A comparison of three trapping methods used to survey forest-dwelling Coleoptera. *Eurasian Journal of Entomology*, **103**, 397–407.

Irmler, U. (2003) The spatial and temporal pattern of carabid beetles on arable fields in northern Germany (Schleswig-Holstein) and their value as ecological indicators. *Agriculture, Ecosystems and Environment*, **98**, 141–151.

Jackson, J.K. & Fureder, L. (2006) Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. *Freshwater Biology*, **51**, 591–603.

Klenner, M. (1989) Uberlebenstrategien einer stenotopen Waldart : Untersuchungen zur Dynalik einer westfalischen *Carabus auronitens* Population (Coleoptera, Carabidae). *Verhandlungen der Gesellschaft fur Okologie* , **18**, 781–791.

Kozlov, M.V., Hunter, M.D., Koponen, S., Kouki, J., Niemela, J. & Price, P.W. (2010) Diverse population trajectories among coexisting species of subarctic forest moths. *Population Ecology*, **52**, 295–305.

Lachat, T., Nagel, P., Cakpo, Y., Attignon, S., Goergen, G., Sinsin, B. & Peveling, R. (2006) Dead wood and saproxylic beetle assemblages in a semi-deciduous forest in Southern Benin. *Forest Ecology and Management*, **225**, 27–38.

Martikainen, P. & Kaila, L. (2004) Sampling saproxylic beetles: lessons from a 10-year monitoring study. *Biological Conservation*, **120**, 175–185.

Martikainen, P. & Kouki, J. (2003) Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodiversity and Conservation*, **12**, 1815–1831.

McArdle, B.A. (1990) When are rare species not there? *Oikos*, **57**, 276–277.

McIntosh, R.L., Katinic, P.J., Allison, J.D., Borde, J.H. & Downey, D.L. (2001) Comparative efficacy of five types of trap for woodborers in the Cerambycidae, Buprestidae and Siricidae. *Agricultural and Forest Entomology*, **3**, 113–120.

Nageleisen, L.M. & Bouget, C. (2009) *Forest Insect Studies: Methods and Techniques. Key Considerations for Standardisation. An Overview of the Reflexions of the 'Entomological Forest Inventories' Working Group (Inv.Ent.For)*. *Les dossiers forestiers n◦19* . Office National des Forets, France.

Niemela, J.K. & Spence, J.R. (1994) Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography*, **17**, 166–175.

Niemela, J., Halme, E., Pajunen, T. & Haila, Y. (1986) Sampling spiders and carabid beetles with pitfall traps: the effect of increased sampling effort. *Annales Entomologici Fennici* , **52**, 109–111.

Niemela, J., Halme, E. & Haila, Y. (1990) Balancing sampling effort in pitfall trapping of carabid beetles. *Entomologica Fennica*, **1**, 233–238.

Niemela, J., Spence, J.R. & Spence, D.H. (1992) Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Canadian Entomologist*, **124**, 521–540.

Nieto, A. & Alexander, K.N.A. (2010) *European Red List of Saproxylic Beetles*. Publications Office of the European Union, Luxembourg. Novotny, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, **89**, 564–572.

Ohsawa, M. (2007) The role of isolated old oak trees in maintaining beetle diversity within larch plantations in the central mountainous region of Japan. *Forest Ecology and Management*, **250**, 215–226.

Økland, B. (1996) A comparison of three methods of trapping saproxylic beetles. *Eurasian Journal of Entomology*, **9**, 195–209.

Oksanen, J., Blanchet, F.G., Kindt, R. *et al*. (2011) *vegan: Community Ecology Package*. R Package Version 2.0-2 [WWW document]. URL http://CRAN.R-project.org/package=vegan [accessed on 1 February 2012].

Ranius, T. (2001) Constancy and asynchrony of *Osmoderma eremite* populations in tree hollows. *Oecologia*, **126**, 208–215.

R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria. [WWW document]. URL http://www.R-project.org [accessed on 1 February 2012].

Rink, M. & Sinsch, U. (2007) Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. *Journal of Zoology*, **272**, 235–243.

Salama, N.K.G., Knowler, J.T. & Adams, C.E. (2007) Increasing abundance and diversity in the moth assemblage of east Loch Lomondside, Scotland over a 35 year period. *Journal of Insect Conservation*, **1 1**, 151–156.

Scott, W.A. & Anderson, R. (2003) Temporal and spatial variation in carabid assemblages from the United Kingdom Environmental Change Network. *Biological Conservation*, **110**, 197–210.

Siitonen, J. (1994) Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. *Annales Zoologici Fennici* , **31**, 89–95.

Stokland, J., Tomter, S. & Soderberg, U. (2004) Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. *Monitoring and Indicators of Forest Biodiversity in Europe – From Ideas to Operationality, EFI Workshop, 12–15 November 2003, Italy* (ed. by M. Marchetti), pp. 207–226. European Forest Institute, Finland.

Sverdrup-Thygeson, A. & Birkemoe, T. (2008) What window traps can tell us: effect of placement, forest openness and beetle reproduction in retention trees. *Journal of Insect Conservation*, **13**, 183–191.

Turchin, P., Taylor, A.D. & Reeve, J.D. (1999) Population cycles of a forest insect: an experimental test. *Science*, **285**, 1068–1071.

White, E.P., Adler, P.B., Lauenroth, W.K., *et al*. (2006) A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos*, **112**, 185–195.

Wikars, L.O., Sahlin, E. & Ranius, T. (2005) A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *Canadian Entomologist*, **137**, 304–324.

Williams, C. (1940) An analysis of four years captures of insects in a light trap. Part 2. The effect of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population. *Transactions of the Royal Entomological Society of London*, **90**, 227–306.

Wood, S.N. (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society B* , **70**, 495–518.

Table 1 Summary of the dataset used for analyses

Dataset	Site	Number of sampling years	Number of species	Number of traps	Number of plots
MYT	BALLONS-COMTOIS*	3	135	12	6(6)
MYT	BANNES*	2	101	4	2(2)
MYT	BELG-WAL	2	116	176	22
MYT	CHALMESSIN*	3	106	4	2(2)
MYT	CHAUMES*	2	47	4	2(2)
MYT	COURNEUVE	2	85	10	2
MYT	FONTBLEAU-OPIE*	2	77	2	1(1)
MYT	HAUTE-MEURTHE*	3	134	4	2(2)
MYT	HAUTS-DE-SEINE*	2	148	16	5(2)
MYT	JUJOLS*	2	78	2	1(1)
MYT	KERTOFF*	3	82	2	1(1)
MYT	LARCHANT-MARAIS*	2	102	4	2(2)
MYT	LOZERE*	2	201	16	10(6)
MYT	MANTET*	2	38	4	2(2)
MYT	RNVA*	3	85	2	1(1)

MYT	SAUSSET	2	105	25	5
MYT	TOURBIERE-CHARMES*	2	62	4	2(2)
MYT	TRONCAIS-ONF*	3	162	6	3(3)
MYT	VAUHALAISE*	2	47	2	1(1)
MTP	AUBERIVE	1	146	48	24
MTP	BELG-WAL	2	81	44	22
MTP	BRIE	1	112	28	14
MTP	CAYLUS	1	93	4	2
MTP	CHAUX-REGIX	1	57	6	3
MTP	EAST-FRANCE	1	210	58	29
MTP	FONTAINEBLEAU	1	188	50	25
MTP	LANDES	1	210	104	52
MTP	ORLEANS	1	125	42	21
MTP	ORLEANS-REGIX	1	95	6	3
MTP	RAMBOUILLET	1	265	120	60
MTP	TRONCAIS-CEM	1	190	62	31
MTP	VENTRON	1	52	16	8

∗Denotes the sites used to compare the number of additional species collected by a second trap in 1-year plots or by a second year of running one trap in 2-year plots. The number of plots used for multi-year comparisons is given in parenthesis in the 'Plot' column. MTP, multi-trap plots; MYT, multi-year traps.

Table 2 Effect of sampling effort per plot (number traps/years) on species richness and assemblage composition at particular sites

	Sites	Comparison between 1 and 2 (years per trap or traps per plot)			
		Number of plots (traps)	SR-Benefit	Mean Mantel statistics r (1 *vs* 1+2)	Mean Mantel statistics r (2 *vs* 1+2)
MYT	Ballons Comtois	6(12)	24.10%	0.78***	0.47***
	Belg-Wal	22(176)	20.21%	0.59***	0.57***
	Courneuve	2(10)	40.50%	0.60***	0.28*
	Hauts-de-Seine	5(16)	35.16%	0.52***	0.60***
	Lozère	10(16)	29.06%	0.86***	0.89***
	Sausset	5(25)	40.94%	0.80***	0.78***
	mean		**31.66%**	**0.69**	**0.60**
MTP	Auberive	24(48)	30.94%	0.64***	0.55***
	Belg-Wal	22(44)	33.88%	0.58***	0.62***
	Brie	14(28)	24.44%	0.79***	0.57**
	Coppices (=East France)	29(58)	23.89%	0.71***	0.73***
	Fontainebleau	25(50)	24.50%	0.71***	0.68***
	Rambouillet	60(120)	27.27%	0.67***	0.65***
	Landes	52(104)	15.72%	0.81***	0.84***
	Troncais-CEM	31(62)	19.87%	0.34***	0.60***
	mean		**25.06%**	**0.6621**	**0.6617**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The mean species richness benefit index (SR-Benefit) (see text) between traps (multi-trap plot; MTP) or years (multi-year trap; MYT) was used to measure the increase in species number caught by one additional trap or year, respectively. Mantel tests (999 permutations) assessed whether within-site

between-trap Sorensen distance matrices based, respectively, on single traps/years were correlated with data that included another trap or year, respectively. The number of traps in parenthesis is the total number of traps per site.

Table 3 Number of traps in multi-year trap (MYT) and multi-trap plot (MTP) datasets for each ecological studied factor

Environmental/methodological factors		Number of traps	
Factor	Category	MYT	MTP
Forest type	Conifer	11	89
	Deciduous	250	459
	Mixed	38	40
Altitude	Highland	44	16
	Lowland	255	572
Climatic domain	Alpine*	6	0
	Atlantic	57	360
	Continental	220	228
	Continental / mediterranean*	16	0
Bait	Alcohol-baited	82	32
	No	217	556

*a*This category was not considered as a result of its low number of replicates

Table 4 Effects of sampling effort per plot (number of traps) on faunistic comparisons of different stand types

			Comparison between A-B stand types			
			1 trap per plot		2 traps per plot	
Stand type	Forests	Number of plots (traps)	Species richness difference	Assemblage [A-B] dissimilarity	Species richness difference	Assemblage [A-B] dissimilarity
A=managed	Auberive	24(42)	10%^{ns}	71.30%	13%^{ns}	65.40%
B=reserve	Fontainebleau	25(50)	-25%^{ns}	78.80%	-27%*	73.12%
A=deadwood-poor	Rambouillet	60(120)	23%^{ns}	66.97%	6%^{ns}	61.41%
	Landes	52(104)	-1%^{ns}	77.96%	-30%*	73.27%
B=deadwood-rich	BelgWal Year1	22(44)	34%^{ns}	75.28%	10%^{ns}	70.33%
	BelgWal Year2	22(44)	-12%^{ns}	82.15%	23%^{ns}	76.52%
A=mature	Coppices (Eastern France)	29(58)	36%*	64.73%	41%*	62.79%
B=overmature	Troncais-CEM	31(62)	-20%^{ns}	68.49%	6%^{ns}	62.49%
	mean		**|20.1%|**	**73%**	**|19.5%|**	**68%**

∗If order-1 Chao estimators of species richness in forest categories A and B did not overlap, not significant (NS) if they overlapped; Sorensen dissimilarity values (+/− SD) did overlap in all comparisons of forest categories A and B with 1 or 2 traps per plot. The difference in species richness (order-1 Chao estimators) was calculated as the percentage of supplementary species in the B compared with the A stand type. Mean values of species richness difference were based on absolute values (|mean value|). Plots were considered to be dead wood-rich, using the thresholds: 30 m3/ha in the Rambouillet oak forest and in the Belgian oak-beech forests, and 20 m3/ha in the French Landes pine forest. Mature high forests were 150–175 years old; overmature high forests were more than 200 years old (Troncais); mature coppices were 25–30 years old, whereas overmature coppices were 70–80 years old (Coppices). The number of traps between brackets is the total number of traps per site.

Figure 1 Mean benefit of species richness (SR-Benefit) values between traps (multi-trap plot; MTP) or years (multi-year trap; MYT) for 'all species', 'common species' and 'rare species'. SR-Benefit is the increase in species number caught by one supplementary trap or year, which are compared as a percentage with one single trap or one single year, respectively. In the MYT between year analyses, we tested the effects of different combinations of 1-, 2- and 3-year sampling designs on SR-Benefit: a second sampling year after the first one (SR-Benefit A), a third sampling year after two first consecutive sampling years (SR-Benefit B), two supplementary sampling years after a single first one (SR-Benefit C). Error bars represent the 95% confidence intervals.

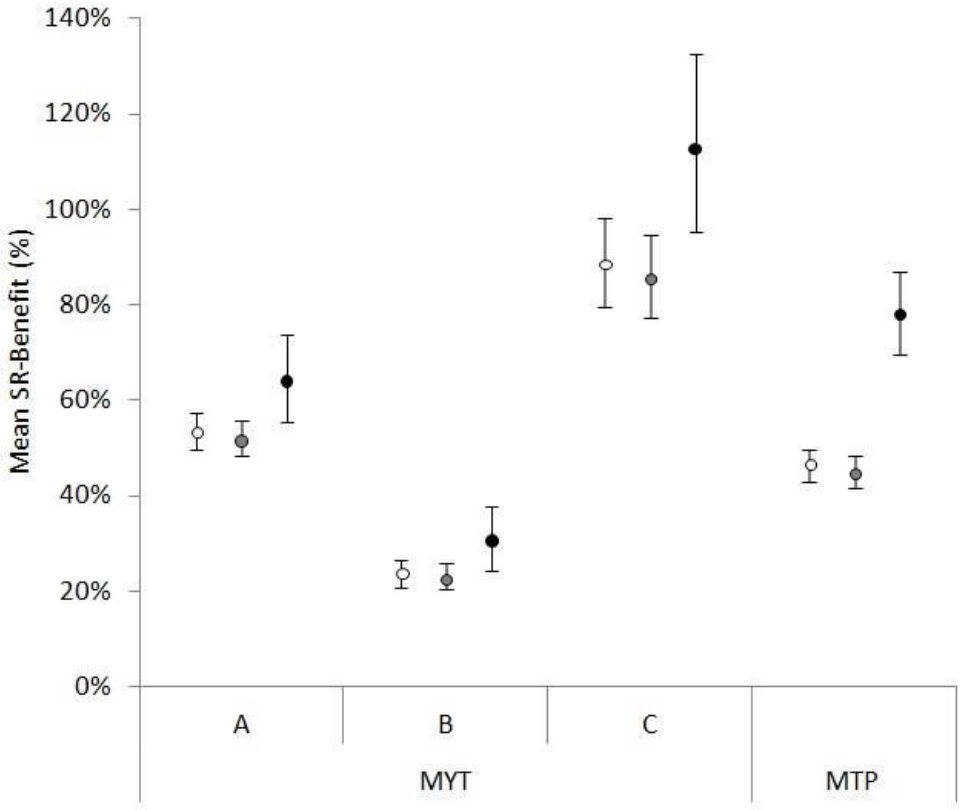


Figure 2 Mean Sorensen dissimilarity between traps (multi-trap plot; MTP) or years (multi-year trap; MYT) for 'all species'. The mean dissimilarity is the difference in species composition between assemblages caught by one single trap or one single year and assemblages caught by two traps or additional years. In the MYT between year analyses, we assessed the dissimilarity between assemblages caught with different combinations of 1-, 2- and 3-year sampling designs: a second sampling year after the first one (dissimA), a third sampling year after two first consecutive sampling years (dissimB), two supplementary sampling years after a single first one (dissimC). In the MTP between trap analyses, 'dissim' is defined as the dissimilarity between assemblages caught by one or two traps. Error bars represent the 95% confidence intervals.

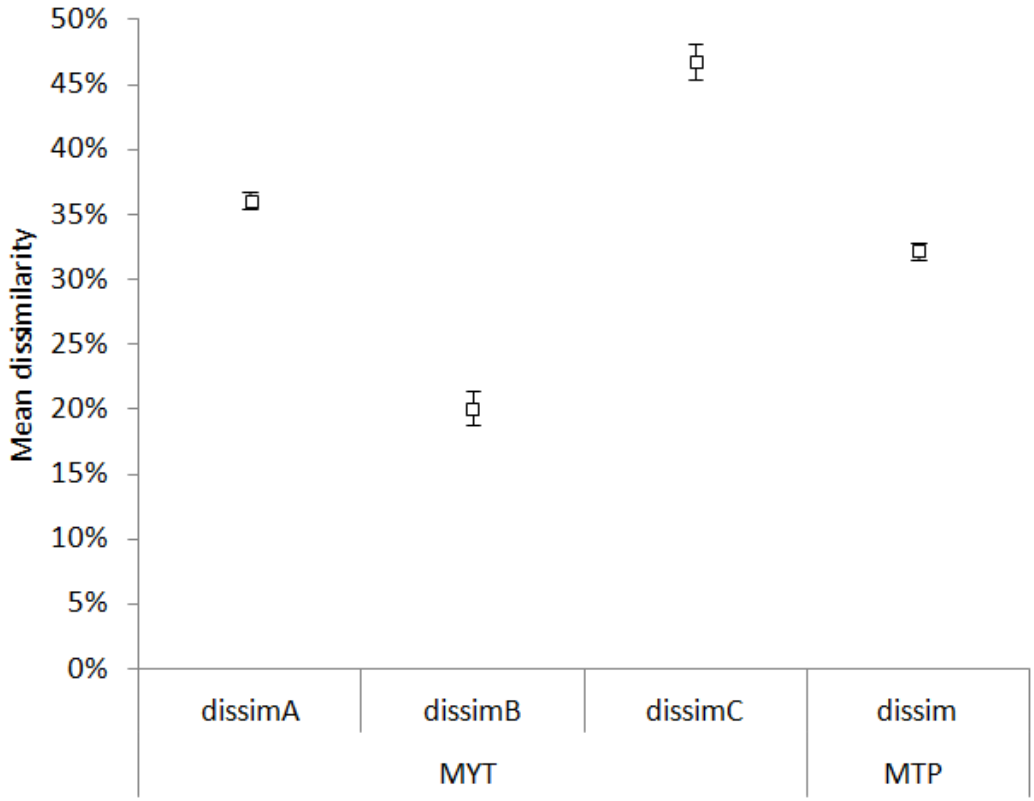
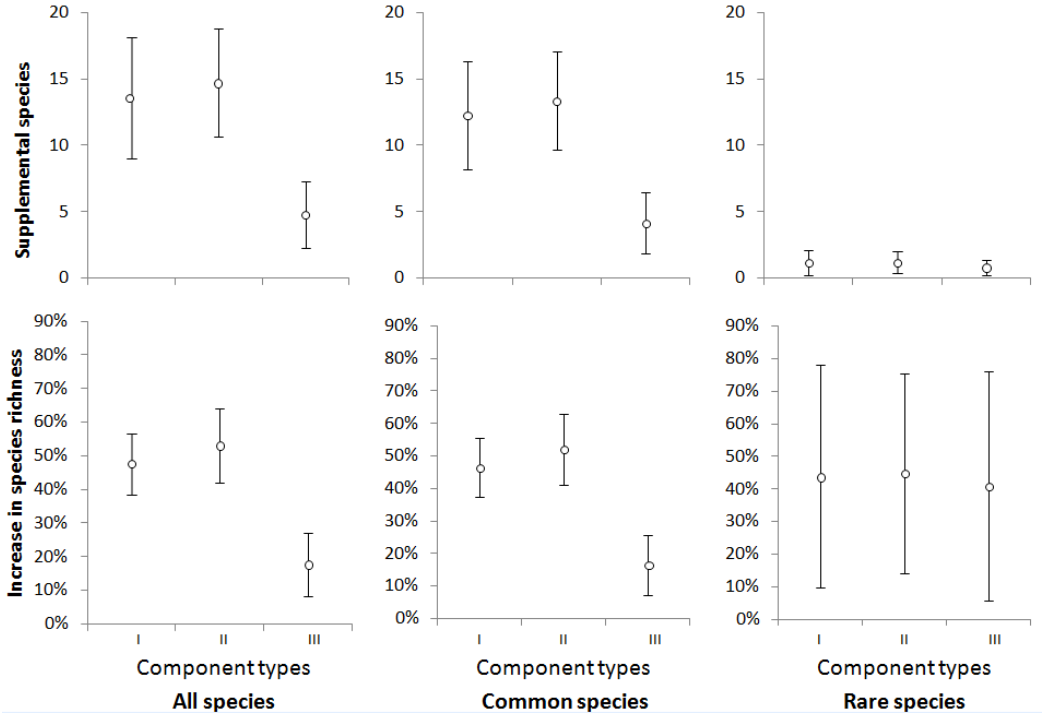


Figure 3 Exclusive and interactive effects of trap or year replication on the total species richness in two-trap and 2-year plot designs, for all, common and rare species (multi-trap-multi-year-plot; MTMYP dataset). The increase in species richness was partitioned into three components: as a result of trap replication exclusively (from one to two traps) (I), as a result of year replication exclusively (from 1 to 2 years) (II) and as a result of both replication modes redundantly (III). Error bars are the SD.



Accepted 22 December 2012 First published online 1 March 2013 The Royal Entomological Society, *Agricultural and Forest Entomology*, **15**, 135–145

Bulletin of Entomological Research (2015) 105, 101–109 doi:10.1017/S0007485314000741 © Cambridge University Press 2014

Article2: Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests?

G. Parmain1,2,3*, C. Bouget1, J. Müller4, J. Horak5, M.M. Gossner6, T. Lachat7 and G. Isacsson8

1National Research Institute of Science and Technology for Environment and Agriculture. (IRSTEA), 'Forest ecosystems' Research Unit, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France: 2National Laboratory of Forest Entomology, National Forest Office (ONF), F-11500 Quillan, France: 3National Museum of Natural History, Natural Patrimony Department, 36 rue Geoffroy St Hilaire, CP 41 75 231 Paris cedex 05, France: 4Nationalparkverwaltung Bayerischer Wald Stellvertretender Leiter Sachgebietsleiter Naturschutz und Forschung Freyunger Str. 2, 94481 Grafenau, Germany: 5Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamycka 1176, CZ-165 21 Prague, Czech Republic: 6Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-vonCarlowitz-Platz 2, 85354 Freising-Weihenstephan, Germany: 7Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland: 8Swedish Forest Agency, P.O. Box 63, SE-281 21 Hässleholm, Sweden

Abstract

Monitoring saproxylic beetle diversity, though challenging, can help identifying relevant conservation sites or key drivers of forest biodiversity, and assessing the impact of forestry practices on biodiversity. Unfortunately, monitoring species assemblages is costly, mainly due to the time spent on identification. Excluding families which are rich in specimens and species but are difficult to identify is a frequent procedure used in ecological entomology to reduce the identification cost. The Staphylinidae (rove beetle) family is both one of the most frequently excluded and one of the most species-rich saproxylic beetle families. Using a large-scale beetle and environmental dataset from 238 beech stands across Europe, we evaluated the effects of staphylinid exclusion on results in ecological forest studies. Simplified staphylinid-excluded assemblages were found to be relevant surrogates for whole assemblages. The species richness and composition of saproxylic beetle assemblages both with and without staphylinids responded congruently to landscape, climatic and stand gradients, even when the assemblages included a high proportion of staphylinid species. At both local and regional scales, the species richness as well as the species composition of staphylinid-included and staphylinid-excluded assemblages were highly positively correlated. Ranking of sites according to their biodiversity level, which either include d or excluded Stap hylinidae in species richness, also gave congruent results. From our results, species assemblages omittin staphylinids can be taken as efficient sur rogates for complete asse mblages in large scale biodiversity monitor ing studies.

Keywords: biodiversity surrogate, insect sampling, biodiversity monitoring, identification cost

Introduction

The importance of beech forests for forest biodiversity conservation in Central Europe has recently been highlighted by several studies (Müller et al., 2013; Lachat et al., 2012; Gossner et al., 2013). Within beech forest biodiversity, deadwood-associated (saproxylic) species account for about 25% of the total species richness occurring in temperate and boreal forest ecosystems (Siitonen, 2001; Stokland et al., 2004). This high proportion makes them challenging candidates for forest biodiversity monitoring. However, the species-rich saproxylic group is often seen as a response group in forest ecology. Furthermore, this group is known to be highly sensitive to forest management and

has consequently become threatened (Nieto & Alexander, 2010). Furthermore, saproxylic organisms may be used to discriminate old-growth forests from managed ones (Siitonen & Saaristo, 2000), or as indicators for different forestry regimes (Davies et al., 2008).

Among the saproxylic organisms, beetles account for more than 20% of the species diversity (Stokland et al., 2004) and are often used as a relevant indicators of forest management impacts for convenience and practical reasons. Monitoring saproxylic beetle diversity has three main objectives: (i) forest site ranking, i.e., sorting sites according to their biodiversity level, and to identify relevant conservation sites (Timonen et al., 2010), (ii) identifying environmental structural drivers of forest biodiversity (Bouget et al., 2014) in order to establish efficient conservation measures and management guidelines, and (iii) assessing the impacts of forest management on biodiversity (Davies et al., 2008).

The monitoring of species assemblages is nonetheless costly, mainly due to difficult and time-consuming species identification (Müller & Brandl, 2009). High resolution analyses require informative long-time and costly datasets. The importance of data quality in saproxylic ecological studies has already been highlighted (Parmain et al., 2013). Several strategies are available to simplify the study of saproxylic species assemblages, especially to reduce the time spent on identification. These strategies imply the identification of specimens (i) at a morphospecies level (Obrist & Duelli, 2010), (ii) a supra-species level (e.g., genus level), or (iii) at the species level for only a species subset (indicators – Schmidl & Bussler, 2004) or selected families or species (monitoring species – Müller & Gossner, 2010).

Morphospecies, instead of species, have been used in order to reduce identification cost, but this seems more efficient for butterflies and spiders (Derraik et al., 2002) than for beetles (Olivier & Beattie, 1996). Supra-species monitoring, also called 'taxonomy sufficiency', is widely used to rapidly assess changes in biodiversity (Beattie & Olivier, 1994), but it does not allow researchers to determine fine-scale changes (Williams & Gaston, 1994) nor can multivariate analyses be computed (Terlizzi et al., 2003). Species subsets may be easier, cheaper and faster to study than the entire target group (Williams & Gaston, 1994), but relevant subsets able to predict overall species richness are difficult to identify. Within the saproxylic beetle group, the explanatory power of several species subsets have already been tested, such as easyto-identify (Sebek et al., 2012) or red-listed species (Timonen et al., 2010; Lachat et al., 2012). A near-full set of species can be quickly obtained while excluding the families whose identification is very time-consuming or taxonomically complicated (Kennedy & Jacoby, 1997). Family exclusion is therefore a frequently used procedure in beetle studies (Grove, 2002; Ohsawa, 2007; Bouget et al., 2014). Most of the excluded families are taxonomically complicated and their biology is not well known. Among saproxylic beetle families, some are nearly always kept for analyses (Cerambycidae, Elateridae, Cetoniidae) whereas others are often excluded from masstrapping samples to exclude doubtful data (Cryptophagus and Atomaria genera in Cryptophagidae, Epuraea in Nitidulidae, Latridiidae and Staphylinidae, especially Aleocharinae). Sebek et al. (2012) explored the surrogate ability of several saproxylic beetle families, either individually or in combination, to estimate total species richness per trap. However, rove beetles (Staphylinidae) were not available in the beetle dataset they used.

The rove beetle family is one of the most species-rich saproxylic beetle families (just behind longhorn beetles. Supplementary Material). Today, staphylinid taxonomy is in effervescence

worldwide, with many new species being described (Brunke et al., 2012). On the other hand, it is also one of the most frequently excluded taxa. In some forest environments, staphylinids are one of the most abundant and species-rich families in trapped saproxylic beetle assemblages (Alinvi et al., 2007; Müller et al., 2008). In addition to their hyper-diversity (they are the most species-rich saproxylic subfamily in western Europe), Staphylinidae are hard to identify for the following reasons: (i) there are very few specialized taxonomical experts (Kim & Byrne, 2006); (ii) identification keys and books are difficult to keep up to date due to the quickly evolving taxonomy (though recent publications (Löbl & Smetana, 2004; Assing & Schülke, 2011) have updated the previous identification tools (Lohse, 1964; Lohse et al., 1974) for Central Europe (excluding, however, some speciesrich sub-families such as Aleocharinae, Pselaphinae and Scydmaeninae); (iii) identification requires the analysis of internal genitalia, i.e., the Aleocharinae, (Schmidl & Bussler, 2004; Bouget et al., 2008; Stokland & Meyke, 2008); and (iv) the few specialists are rapidly overwhelmed by the huge quantities of samples related to large-scale sampling designs (Langor et al., 2006).

These reasons all indicate that excluding Staphylinidae from forest biodiversity samples may save time and money and make saproxylic beetle datasets more rapidly available for analysis. Nonetheless, the effects of such an exclusion on the results in ecological studies must be evaluated.

Using a large-scale dataset compiled in European beech forests (Müller et al., 2013), we addressed the following main questions:

- Do saproxylic beetle assemblages with and without staphylinids congruently respond to ecological (landscape, macroclimatic and local) gradients? How do the species richness and composition of assemblages with and without staphylinids co-vary? In addition, we analyzed this secondary issue: Is the response of staphylinid-restricted assemblages to ecological gradients well reflected by the response of staphylinid-excluded assemblages?

Material and methods

We compiled saproxylic beetle data obtained during various projects and corresponding to a total of 1188 flight interception traps in 238 forest stands dominated by European Beech (> 50% beech cover) on 85 sites in nine different countries (see Supplementary Material) from Sweden to Switzerland and the Ukraine (Carpathians). All traps were cross-vane flight-interception traps made up of transparent plastic windows, with total interception area comprised between 0.6 and 1 m2.

Ecological gradients and environmental data

For the purpose of this study, forest conditions were surveyed at the following levels (see Gossner et al., 2013, for details):

(i) Landscape characteristics (see table 1) (3-km radius around the center of each stand) were assessed according to the European-wide land-cover mapping project CORINE (http://www.corine.dfd.dlr.de), which uses satellite remote-sensing images at a scale of 1:100,000. Land-use information includes 44 categories, which were used to calculate the following variables (table 1): the proportion of deciduous forest, the proportion of conifer stands relative to the extent of forest and the proportion of traffic and

settlements. For Switzerland, the variables were taken from www.swisstopo.admin.ch; for Ukraine, the variables were estimated from Google Earth aerial photos.

(ii) Climate variables (see table 1) were extracted from the WorldClim database with a resolution of 30 s and calculated as a mean value within a 1-km radius; a larger radius would have led to inaccurate values for sites in rough terrain (Hijmans et al., 2005). We selected mean temperature and precipitation of warmest quarter as ecologically meaningful variables for the life cycle of beetles. In addition, we included trap elevation.

(iii) Stand conditions (see table 1) were defined according to three parameters: the estimated deadwood amount in three levels (low (< 30 m3 ha 1; N=689), medium (30–70 m3 ha 1; N=257), high (> 70m3 ha 1; N=242)), the protection status (managed versus unmanaged; a stand was considered unmanaged only if harvesting had been absent for at least 10 years), and the occurrence of veteran trees in the trap surroundings (presence versus absence).

Beetle data

Beetles were identified to the species level by taxonomic experts, and only saproxylic species were considered for our analyses. We classified beetles as saproxylic following Schmidl & Bussler (2004) and Köhler (2010).

We defined three types of species assemblage: (i) with Staphylinidae only (staphylinid-restricted), (ii) with all species except for Staphylinidae (staphylinid-excluded), and (iii) with all species including Staphylinidae (staphylinid-included).

We distinguished three levels of Staphylinidae species richness per trap: low (staphylinid species accounted for <10% of total trap richness; N= 466)), medium (staphylinid richness = 10–25% of total richness; N= 521)) and high (> 25% of the species were Staphylinidae, N= 201).

Analyses

Most analyses were carried out at the trap level. The European dataset was divided into eight regions, defined by hierarchical cluster analysis (HCA) of between-trap Euclidian distance matrices between geographical coordinates (vegdist function, lme4 package (Bates et al., 2014)) (Supplementary Material). These geographical clusters were included in our models as random spatial effects.

The correlations between staphylinid-restricted/staphylinid-excluded and staphylinid-included/staphylinid-excluded species richness were calculated with Spearman correlation tests.

We also analyzed the effects of staphylinid exclusion on site ranking, based on species richness. We ranked forest sites (regional scale) and stands (local scale) according to the species richness of staphylinid-included or staphylinid-excluded assemblages. We used the ‘min’ method in the rank R function to manage ties (ex-aequos). At both spatial scales (forest n = 85 and stand n = 238), we computed the mean absolute value of rank differences (standardized by sample size) and the total percentage of congruent rankings (± 5% ranking error). After ranking, we also quantified how much the top-ten forests (or sites, or stands) diverge using staphylinidae-excluded or -included species richness values.

Contributions of environmental variables (climate, landscape and stand variables; table 1) to variations in species richness (rarefied by abundance) between staphylinidrestricted/staphylinid-excluded and staphylinid-included/ staphylinid-excluded assemblages were analyzed in Linear Mixed Models, with country, forest site and stand as spatiallyimplicit random effects on the intercept (glmer function in lme4 (Bates et al., 2014)).

Compositional differences between staphylinid-restricted/staphylinid-excluded and staphylinid-included/staphylinidexcluded assemblages were analyzed using spatiallyconstrained Mantel tests (method = 'pearson', permutation = 999, strata = region). To rank the effect of several variables on variations in species composition (including singletons), we performed a canonical analysis of principal coordinates (CAP) (vegan R-package, Anderson & Willis, 2003) with 'forest' as a constrained factor. Based on Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, since co-linearity among predictor variables is not considered to be a problem in CAP. We calculated the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance (permutation tests – 199 runs), and the relative contribution of each set of variables to marginal inertia.

All analyses were conducted with R 3.0.1 (R Core Team, 2013).

Results

Our compiled dataset included 552,651 individuals and 936 saproxylic beetle species. Staphylinidae was the most species-rich family (145 species). These 145 staphylinid species account for about 16% of the cumulated richness and 14% of the mean richness per trap. The contribution of rove beetles to the mean species richness per trap was not different in managed or in unmanaged stands, in deciduous- or in coniferdominated forests, in deadwood-poor or in deadwood-rich stands, and in lowland or in mountain forests (for details, see Supplementary Material).

(1) Staphylinid-included versus staphylinid-excluded assemblages

Alpha diversity and stand ranking

At the stand level, the Spearman correlation value between species richness in staphylinid-included versus staphylinidexcluded assemblages was very high (rho = 0.99; fig. 1 a). The ten most species-rich stands were consistent between staphylinid-included and staphylinid-excluded assemblages for nine out of ten stands. The stand ranking based on staphylinidexcluded data gave a similar result compared with staphylinid-included data in more than 75% of the cases, considering a 5% ranking error; respectively 77 and 79% of the cases in managed and unmanaged stands. The mean value of rank difference between staphylinid-included and staphylinidexcluded ranking standardized by sample size was 0.03, both in managed and unmanaged stands. The Mantel correlation value between staphylinid-included and staphylinid-excluded dissimilarity matrices was high and significant ($r = 0.98$, $P < 0.001$; fig. 1 b).

Gamma diversity and site ranking

At the forest site level, species richness in staphylinidincluded and staphylinid-excluded assemblages was strongly correlated (Spearman rho = 0.99; fig. 1 c). The identification of the ten most species-rich sites in our dataset was similar with staphylinid-excluded data compared with staphylinidincluded data in more than 75% of the cases (with an accepted 5% ranking error). In the Top10 sites given by the ranking of staphylinid-excluded assemblages, eight were also among the Top10 based on staphylinid-included data. The mean value of rank difference between staphylinid-included and staphylinid-excluded data ranking, standardized by sample size, was 0.03.

Environmental drivers of variations in species richness

Whether staphylinid-included or -excluded datasets were used, the influence of structural variables on species richness was consistent. Furthermore, the proportion of variance explained by fixed factors (for significant factors only, R2) was slightly higher for staphylinid-excluded data (Supplementary Material). The level of staphylinid richness per trap did slightly influence the response of beetle species richness to environmental parameters. In the dataset restricted to traps with low or medium staphylinid richness, the effects of stand, climatic and landscape variables on species richness per trap were always consistent between staphylinid-included and staphylinid-excluded assemblages. However, in the case of traps with high staphylinid richness, the effect of the climatic variable, mean temperature of the warmest quarter, was significant on the staphylinid-excluded assemblage, but not on the whole assemblage.

Environmental drivers of variations in species composition

From the CAP results, a uniform and significant response of the intrinsic contributions to inertia of selected variables was observed with both the staphylinid-included and the staphylinid-excluded species assemblages. Deadwood amount was the most powerful explanatory variable (table 3).

(2) Response of staphylinid-restricted assemblages

At the stand level, the Spearman correlation value between species richness in staphylinid-restricted versus staphylinidexcluded assemblages was lower than the staphylinidincluded/staphylinid-excluded correlation but remained significant (rho=0.74; fig. 1d). The Mantel correlation value was low but still significant between staphylinid-restricted and staphylinid-excluded distance matrices (r=0.18, P<0.001; fig. 1e). At the forest site level, species richness values were less correlated in staphylinid-restricted versus staphylinidexcluded assemblages (rho=0.78; fig. 1f) than in staphylinidincluded versus staphylinid-excluded assemblages.

Environmental drivers of variations in species richness

The effects of stand, climatic and landscape variables on species richness per trap were not always consistent between staphylinid-restricted and staphylinid-excluded assemblages (table 2). Deadwood amount and mean temperature of the warmest quarter had a significant effect on species richness per trap in the staphylinid-excluded data, whereas they did not significantly affect the species richness per trap in the staphylinid-restricted data.

Environmental drivers of assemblage variations

In comparison with staphylinid-excluded assemblages, staphylinid-restricted assemblages were far less influenced by selected environmental variables: five out of nine predictors did not have a significant intrinsic contribution to inertia (table 3). Unlike staphylinid-excluded assemblages, staphylinid-restricted assemblages were not significantly influenced by management treatment by a surrounding landscape cover of conifer-dominated forests or by bio-climatic variables (table 3). Like staphylinid-excluded assemblages, staphylinid-restricted assemblages were affected by a surrounding landscape cover of deciduous-dominated forests, by local deadwood amount and by local occurrence of veteran trees. As for staphylinid-excluded assemblages, deadwood amount had the most important intrinsic contribution to inertia.

Mean temperature and deadwood amount did significantly affect the species richness of staphylinid-excluded assemblages, but not of staphylinid-restricted assemblages.

Discussion

To include or exclude staphylinids?

In beech-dominated forests, the contribution of rove beetles to the species richness of saproxylic beetle assemblages was important on average, and particularly so in managed stands, in deciduous-dominated landscapes, in deadwoodpoor forests and in lowlands. This shows the important role rove beetles should play in biodiversity monitoring in managed forests at low altitudes; however, these types of forests are not currently the focus of much recent research (e.g., Carnus et al., 2006). These findings clearly support the interest of our study on the impact on ecological results of taking into account this species-rich family or not.

From our evaluation of the effects of Staphylinidae family exclusion on results in ecological studies, we can infer that simplified staphylinid-excluded assemblages are relevant surrogates for whole assemblages. The species richness and composition of assemblages with or without staphylinids consistently co-varied. At the stand and forest site levels, the species richness values of the total assemblage and the staphylinid-excluded assemblage were highly positively correlated. Ranking procedures, with and without Staphylinidae included in species richness, gave consistent and similar results at both local and regional scales. The congruency of stand ranking using the whole or the staphylinid-excluded data for species richness calculations was the same in unmanaged and in managed stands. Moreover, the distance matrices based on both types of assemblages also strongly correlated. Indeed, species richness and composition of saproxylic beetle assemblages, with or without staphylinids, congruently responded to landscape, climatic and stand gradients. The staphylinid-included and the staphylinidexcluded assemblages were generally influenced by similar environmental drivers (deadwood amount, temperature, and elevation), with a greater part of variance explained for staphylinid-excluded assemblages. Therefore, the difference in R2 between models based on staphylinid-included or excluded datasets was low, and we cannot draw conclusions on this point.

Overall, excluding Staphylinidae from saproxylic beetle assemblages did not lead to irrelevant estimations at local or regional scales, contrary to analyses based on data from poorly replicated

designs (Parmain et al., 2013). Olivier & Beattie (1996) obtained similar identical rankings between sites with a simplified morphospecies approach compared with a detailed species inventory.

Staphylinids as a target group?

Since rove beetle species are numerous, easily caught in window-flight traps in various forest conditions, the Staphylinidae family could legitimately be suggested as a potential surrogate group reflecting saproxylic beetles as a whole. Indeed, they are often used in other types of monitoring (e.g., pitfall traps; Buse & Good, 1993). Nevertheless, according to our results in European beech forests, the response of staphylinid-restricted assemblages to rough ecological gradients did not reflect the response of other saproxylic beetle families, though at the stand and the forest site levels, their species richness was significantly correlated. While investigating the surrogate power of four other single saproxylic beetle families, Sebek et al. (2012) observed the highest correlation between within-family and total richness for Cerambycidae (rho =0.50). In our study, we found higher correlation values for Staphylinidae (rho= 0.68). However, the environmental drivers of species richness and composition of staphylinid-excluded or staphylinid-restricted assemblages differed. Moreover, the distance matrices based on the two types of assemblages converged only slightly.

Even though Bohac (1999) proposed the use of rove beetle assemblages as bio-indicators for human land use in seminatural and urban areas, we do not recommend their use as indicators of saproxylic assemblages in a forest context.

Perspectives

We studied saproxylic beetle assemblages only in terms of species richness and composition. Further approaches could focus on the guild structure and the conservation interest of the community. Such research would need to confront the lack of knowledge on rove beetle biology and rarity status. Furthermore, the data that do exist indicate that staphylinid species that have been recorded as predators specialists are probably more opportunistic than was predicted (e.g., Horák et al., 2011). Furthermore, as alluded to in the introduction, many staphylinid species have undescribed larvae and the females of several species are not distinguishable from other species (e.g., Scaphisoma sp.). Staphylinidae are known to have large ecological niches (Bohac, 1999); most of them live in highly variable environments as generalist predators in soil litter or as parasitoids of Dipteran pupae (i.e., Aleocharinae). Their detailed ecological requirements and association to deadwood microhabitats, as well as their rarity status and distribution patterns remain poorly known for many species. Falsely identified saproxylic staphylinid species may therefore weaken, disturb or, in the worst case, invert the relationships pattern between species and environmental conditions. Further ecological and taxonomical research on Staphylinidae is thus urgently needed.

The saproxylic beetle group is family-rich, with more than 70 families in France alone (Bouget et al., 2008). Beetle families other than Staphylinidae may also be time-consuming to identify, and are sometimes excluded from assemblage analyses. These neglected families may concern key feeding groups of specialized species, such as Ciidae, a fungus-eating species, or they may include threatened and often regionally red-listed species such as Aderidae. Their exclusion may lead to biases in the identification of conservation sites and in functional community analyses. The costs and

benefits of family exclusion versus exhaustiveness in beetle biodiversity assessment – especially rapid biodiversity assessments (Sebek et al., 2012) – should be further investigated. Finally, our study was based only on European beech forests, and it would be informative to conduct similar analyses in differing forest settings, for instance in European temperate oak forests or in conifer-dominated boreal forests.

The supplementary material for this article can be found at http://www.journals.cambridge.org/BER.

Acknowlodgements

We are grateful to Y. Paillet, B. Nusillard, C. Moliard (Irstea), T. Noblecourt, T. Barnouin, F. Soldati (ONF), F. Köhler, U. Bense, L. Zapponi, H. Bussler, and all the local forest managers for their field and laboratory work, to F. Gosselin (Irstea) for helpful comments on statistical analyses, L. Cizek and J. Schlaghamerský for helpful comments on a previous draft of the paper, and to Vicki Moore who checked the English language. We are undebtfull to two anonymous reviewers for their helpful comments. Data collection in Italy was supported by the LIFE project ManFor C.BD. (LIFE09 ENV/IT/000078). This study was partly supported by CIGA Cˇ ZU 20144302 'Managed forests in lowlands and their potential from the perspective of two distinct taxa – beetles and birds'.

References

Alinvi, O., Ball, J., Danell, K., Hjältén, J. & Pettersson, R. (2007) Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. Journal of Insect Conservation 11, 99–112.

Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525.

Assing, V. & Schülke, M. (eds) (2011) Die Käfer Mitteleuropas. Band 4. Staphylinidae I. Zweite Neubearbeitete Auflage. Heidelberg, Spektrum Akademischer Verlag, I-XII, pp. 1–560.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) Lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0–6. Available online at http://CRAN.R-project. org/package=lme4

Beattie, A.J. & Olivier, I. (1994) Taxonomic minimalism. Trends in Ecology and Evolution 9, 488–490.

Bohac, J. (1999) Staphylinid beetles as bioindicators. Agriculture, Ecosystems and Environment 74, 357–372.

Bouget, C., Brustel, H. & Zagatti, P. (2008) The French Information System on Saproxylic BEetle Ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation status. Revue Ecologie (Terre et Vie) 63, 25–28.

Bouget, C., Larrieu, L. & Brin, A. (2014) Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecological Indicators 36,656–664.

Brunke, A., Klimaszewski, J. & Anderson, R.S. (2012) Present taxonomic work on Staphylinidae (Coleoptera) in Canada: progress against all odds. ZooKeys 186, 1–5.

Buse, A. & Good, J.E.G. (1993) The effects of conifer forest design and management on abundance and diversity of rove beetles (Coleoptera: Staphylinidae): implications for conservation. Biological Conservation 64, 67–76.

Carnus, J.M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A. & Walters, B. (2006) Planted forests and biodiversity. Journal of Forestry 104, 65–77.

Davies, Z.G., Tyler, C., Stewart, G.B. & Pullin, A.S. (2008) Are current management recommendations for saproxylic invertebrates effective? A systematic review. Biodiversity and Conservation 17, 209–234.

Derraik, J.G.B., Closs, G.P., Dickinson, K.J.M., Sirvid, P., Barratt, B.I.P. & Patrick, B.H. (2002) Arthropod morphospecies versus taxonomic species: a case study with araneae, coleoptera, and lepidoptera. Conservation Biology 16, 1015–1023.

Gossner, M.M., Lachat, T., Brunet, J., Isacsoon, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W. & Müller, J. (2013) Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology 27, 605–614.

Grove, S.J. (2002) The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation 104, 149–171.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965–1978.

Horák, J., Chobot, K., Gabriš, R., Jelínek, J., Konvicˇka, O., Krejcˇík, S. & Sabol, O. (2011) Uphill distributional shift of endangered habitat specialist. Journal of Insect Conservation 15, 743–746.

Kennedy, A.D. & Jacoby, C.A. (1997) Biological indicators of marine environmental health: Meiofauna – A neglected benthic component? Environmental Monitoring and Assessment 54, 47–68.

Kim, K.C. & Byrne, L.B. (2006) Biodiversity loss and the taxonomic bottleneck: emerging biodiversity science. Ecological Researches 21, 794–810.

Köhler, F. (2010) DieklimabedingteVeränderungderTotholzkäferfauna (Coleoptera) des nördlichen Rheinlandes – Analysen zur Gesamtfauna und am Beispiel von Wiederholungsuntersuchungen in ausgewählten Naturwaldzellen. Arnberg, Germany, Landesbetrieb Wald und Holz NRW.

Lachat, T., Wermelinger, B., Gossner, M.M., Bussler, H., Isacsson, G. & Müller, J. (2012) Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecological Indicators 23, 323–331.

Langor, D.W., Spence, J.R., Hammond, H.E., James, J.J. & Cobb, T.P. (2006) Maintaining Saproxylic insects in Canada's extensively managed boreal forests: a review. pp. 109 in Grove, S.J. & Hanula, J.L. (Eds), Insect Biodiversity and Dead Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS–93. Asheville, NC, U.S. Department of Agriculture, Forest Service, Southern Research Station.

Löbl, I. & Smetana, A. (2004) Catalog of the Palaearctic Coleoptera, Volume 2 – Hydrophiloidea, Histeroidea, Staphylinoidea, pp. 942 Stenstrup, Apollo Books.

Lohse, G.A. (1964) Staphylinidae I. (Micropeplinae bis Tachyporinae). pp 364 in Freude, H., Harde, W., Lohse, G.A. (Eds), Die Kafer Mitteleuropas. Krefeld, Goecke and Evers.

Lohse, G.A., Benick, G. & Likovsky, Z. (1974) Staphylinidae II. (Hypocyphtinae bis Aleocharinae). pp. 304 in Freude, H., Harde, W. & Lohse, G.A. (Eds), Die Kafer Mitteleuropas.

Krefeld, Goecke and Evers. Müller, J. & Brandl, R. (2009) Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. Journal of Applied Ecology 46, 897–905.

Müller, J. & Gossner, M. (2010) Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. Biological Conservation 143, 625–633.

Müller, J., Brunet, J., Brin, A., Bouget, C., Brustel, H., Bussler, H., Förster, B., Isacsson, G., Köhler, F., Lachat, T. & Gossner, M.M. (2013) Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. Insect Conservation and Diversity 6, 162–169.

Müller, J., Bussler, H. & Kneib, T. (2008) Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. Journal of Insect Conservation 12, 107–124.

Nieto, A. & Alexander, K.N.A. (2010) European Red List of Saproxylic Beetles, p. 56. Luxembourg, Publications Office of the European Union.

Obrist, M.K. & Duelli, P. (2010) Rapid biodiversity assessment of arthropods for monitoring average local species richness and related ecosystem services. Biodiversity and Conservation 19, 2201–2220.

Ohsawa, M. (2007) The role of isolated old oak trees in maintaining beetle diversity within larch plantations in the central mountainous region of Japan. Forest Ecology and Management 250, 215–226.

Olivier, I. & Beattie, A.J. (1996) Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology 10, 99–109.

Parmain, G., Dufrêne, M., Brin, A. & Bouget, C. (2013) Influence of sampling effort on saproxylic beetle diversity assessment: implications for insect monitoring studies in European temperate forests. Agricultural and Forest Entomology 15, 135–145.

R Core Team. (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at URL http://www.R-project. org/.

Schmidl, J. & Bussler, H. (2004) Ökologische Gilden xylobionter Käfer Deutschlands und ihr Einsatz in der landschaftsökologischen Praxis – ein Bearbeitungsstandard. Naturschutz und Landschaftsplanung 36, 202–218.

Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F., Meriguet, B., Micas, L., Noblecourt, T., Rose, O., Velle, L. & Bouget, C. (2012) A test for assessment of saproxylic beetle biodiversity using subsets of "monitoring species". Ecological Indicators 20, 304–315.

Siitonen, J. (2001) Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecological Bulletins 49, 11–41.

Siitonen, J. & Saaristo, L. (2000) Habitat requirements and conservation of Pytho kolwensis, a beetle species of old-growth boreal forest. Biological conservation 94, 211–220.

Stokland, J.N. & Meyke, E. (2008) The Nordic saproxylic database: an emerging overview of the biological diversity in dead wood. Revue d'Écologie (Terre Vie) 63, 29–40.

Stokland, J., Tomter, S. & Söderberg, U. (2004) Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. pp. 207–226 in Marchetti, M. (Ed.) Monitoring and Indicators of Forest Biodiversity in Europe – From Ideas to Operationality, Vol. 51. EFI workshop, November 12th–15th 2003, Firenze, Italy.

Terlizzi, A., Bevilacqua, S., Fraschetti, S. & Boreo, F. (2003) Taxonomic sufficiency and the increasing insufficiency of taxonomic expertise. Marine Pollution Bulletin 46, 556–561.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Svedrup-Thygeson, A. & Mönkkönen, M. (2010) Woodland key habitats in northern Europe: concepts, inventory and protection. Scandinavian Journal of Fores1t Research 25, 309–324.

Williams, P.H. & Gaston, K.J. (1994) Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? Biological Conservation 67, 211–217.

Table 1. Description of variables (macro-climate, stand, region and landscape) explored in the study. See Gossner et al. (2013) for further details.

			min	mean (sd)	max
Climatic	bio_10	Mean temperature of warmest quarter	116.5	158.1 (10.80)	184.7
	bio_18	Precipitation of warmest quarter	165.8	310.4 (65.48)	434.4
Landscape	Laub3000	On a 3km radius around the center of each stand: proportion of deciduous forest	0.005	0.4205 (0.233)	1
	Nadel3000	On a 3km radius around the center of each stand: proportion of conifer forest	0	0.1931 (0.187)	0.74
	Siedlung3000	On a 3km radius around the center of each stand: proportion of traffic and settlements	0	0.03 (0.049)	0.31
Region	1	Belgium, North-western Germany, Luxembourg	n=512		
	2	Western Germany, Switzerland	n=205		
	3	Sweden	n=70		
	4	Czech Republic, Slovakia	n=50		
	5	Czech Republic, Southern Germany	n=164		
	6	Germany	n=95		
	7	Italy	n=83		
	8	Ukraine	n=9		
Stand	Deadwood amount	Dead wood volume estimation in a 25m radius around the trap.	Low (<30 m^3/ha; N = 689), Medium (30-70 m^3/ha; N = 257), High (>70 m^3/ha; N = 242)		
	Protection	Considered unmanaged only if no harvesting had occurred for at least 10 years	N Unmanaged=339 N Managed=849		
	Veteran Tree	Presence of veteran tree in the surroundings of the trap. Veteran trees have a DBH>70	N Presence=447; N Absence=741		
	Elevation	Altitude of the stand	Plain N=404 Hill N=608 Mountain N=176		
Bio-region		Alpine	n=103		
		Atlantic	n=14		
		Continental	n=1062		
		Mediterranean	n=9		

Table 2. Response in species richness of staphylinid-included, staphylinid-excluded and staphylinid-restricted assemblages to macro-climate, stand and landscape variables, analyzed using a Generalized Linear Mixed Model with a Gaussian error distribution, and forest site and stand as spatial random effects.

Trap subsets	**Species assemblages**	**Ntraps**	**Deadwood amount**	**Elevation**	**Protection**	**Veteran trees**	**bio_10**	**bio_18**	**Laub3000**	**Nadel3000**	**Siedlung3000**
All	Staphylinid-included	1188	**	***			**	***			
	Staphylinid-excluded		**	***			**	***			
	Staphylinid-restricted			***				***			
Low contribution of rove beetles to total richness (0/10%)	Staphylinid-included	466									
	Staphylinid-excluded										
	Staphylinid-restricted										
Medium contribution of rove beetles to total richness (10/25%)	Staphylinid-included	521	**	***			**	***			
	Staphylinid-excluded		**	***			**	***			
	Staphylinid-restricted		**	***				***			
High contribution of rove beetles to total richness (more than 25%)	Staphylinid-included	201		***							
	Staphylinid-excluded			***			**	**			
	Staphylinid-restricted			***				**			

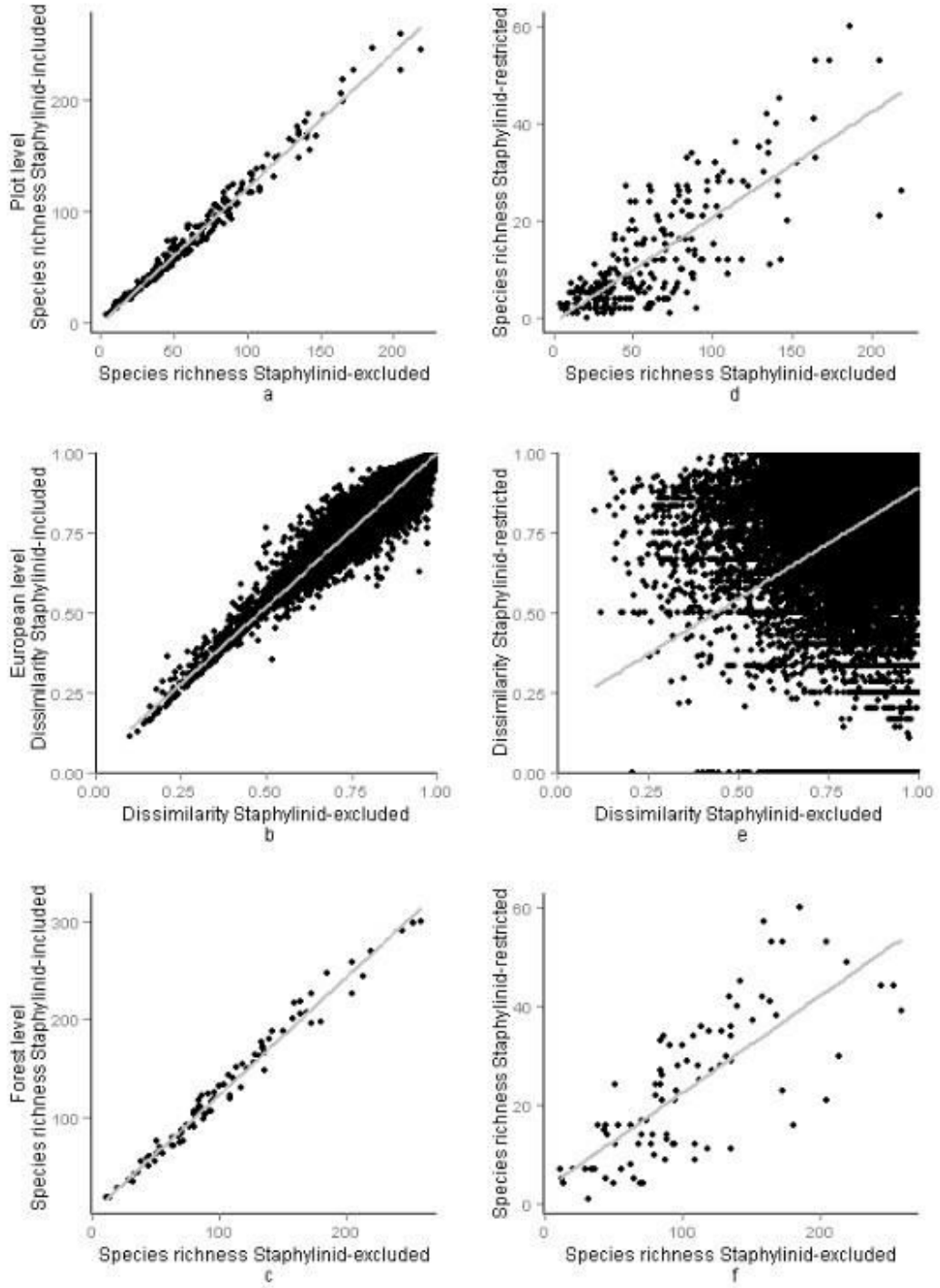
Only significant responses were displayed (***P<0.001, ** 0.01>P>0.001, * 0.05>P>0.01). bio_10, mean temperature of the warmest quarter; bio_18, precipitation of the warmest quarter;Deciduous3000 m, proportion of deciduous forest in a 3km-radius buffer; Conifer3000 m, proportion of conifer forest in a 3km-radius buffer; Urban3000 m, proportion of traffic and settlements in a 3km-radius buffer; Ntraps, number of traps in each Trap subset.

Table 3. CAP used to partition the variation in the response species-plot matrix with respect to the combination of explanatory variables (macro-climate, stand and landscape). Only the intrinsic contribution to inertia of each variable is displayed.

	All species			No staph			Staph only		
	Var	%	signif	Var	%	signif	Var	%	signif
Deadwood amount	**1.69**	**0.44**	******	**1.7**	**0.43**	******	**1.61**	**0.49**	******
Protection	1.14	0.29	**	1.19	0.3	**	0.34	0.1	ns
Elevation	0.9	0.23	**	0.91	0.23	**	0.43	0.13	*
Veteran Trees	0.94	0.24	**	0.93	0.24	**	0.65	0.2	**
bio_10	0.71	0.18	**	0.71	0.18	**	0.41	0.12	ns
bio_18	0.81	0.21	**	0.82	0.21	**	0.38	0.12	ns
Laub3000	0.89	0.23	**	0.89	0.23	**	0.67	0.2	**
Nadel3000	0.58	0.15	**	0.6	0.15	**	0.29	0.09	ns
Siedlung3000	0.58	0.15	**	0.57	0.15	**	0.32	0.1	ns

Signif. codes: ***P <0.001, ** 0.01>P > 0.001, * 0.05>P >0.01, ns P > 0.

Fig. 1. a; b; c: correlation between staphylinid-included and staphylinid-excluded data. d; e; f: correlations between staphylinid-restricted and staphylinid-excluded data.



Partie II : Critiques et perspectives

I) Limites des actions menées

I.1) Réplications spatiale et temporelle

I.1.1) Les différents types de pièges

Nous avons choisi d'étudier les effets de la réplication spatiale et temporelle des pièges à interception sur les cortèges d'espèces saproxyliques obtenus. Bien que cette méthode d'échantillonnage soit dominante en Europe pour ce groupe, il ne faut pas négliger les méthodes complémentaires. Parmi ces dernières, le piège-fosse installé dans les cavités d'arbres (Chiari *et al.,* 2012), les pièges-vitre insérés dans les fructifications de champignons saproxyliques (Kaila, 1993) sont des méthodes susceptibles de réagir différemment à la réplication spatiale ou temporelle.

Cette constatation ne se limite pas aux coléoptères saproxyliques. La connaissance des biais et des efficacités des méthodes de piégeage devrait être généralisée à la totalité des études portant sur les insectes, et de manière plus large sur la totalité des études portant sur les êtres vivants. Cela pour éviter de constater que les résultats mis en évidence par le moyen de certaines méthodes s'avèrent impactées par la méthode d'étude elle-même. Des exemples particulièrement frappants sont produits par Dugger *et al,* (2006) et Beaulieu *et al,* (2010).

I.1.2) Suivis à long terme

Notre étude a été limitée par les données dont nous avons pu disposer. Elles étaient issues d'inventaires, généralement conduits sur de périodes de trois ans, avec un nombre de pièges limités. Nous n'avons de ce fait pas eu accès à des plus grandes séries temporelles. Ces séries temporelles auraient permis de mieux appréhender le changement en composition et en nombre d'espèces supplémentaires contactées au fur et à mesure du temps.

I.1.3) Richesse cumulée

L'évaluation de la quantité d'espèces contactée par rapport au nombre d'espèces présentes dans le milieu se fait généralement par l'utilisation de courbes de richesse cumulées. L'asymptote s'obtient lorsque la quasi-totalité des espèces du milieu a été contactée. A ce moment, l'échantillonnage est jugé représentatif de la communauté étudiée, et les résultats obtenus sont valables pour l'ensemble de la communauté étudiée.

L'effort d'échantillonnage à fournir à l'aide de pièges à interceptions pour contacter 90% d'espèces détectables au Polytrap™ (et non pas du nombre d'espèces total du milieu) n'a pour l'instant pas été évalué. Il faudrait mener une étude de très long terme avec un grand nombre de pièges sur une surface forestière restreinte pour obtenir des premiers résultats. A titre d'exemple, j'expose la courbe de richesse cumulée obtenue avec un échantillonnage effectué à l'aide de 81 pièges à interception (Figure 5a), et l'extrapolation de cette courbe à l'aide de l'équation fournie par la droite de régression (Figure 5b).

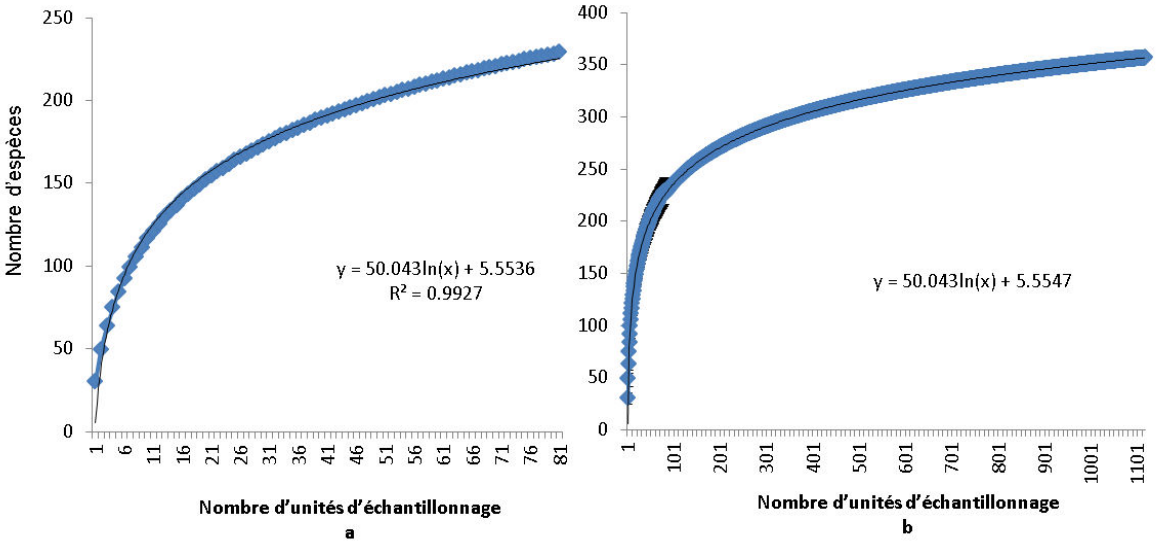


Figure 6 : a : Courbe de richesse cumulée obtenue avec 81 pièges Polytrap™ en fonctionnement pendant une saison biologique. **b :** extrapolation à un grand nombre de pièges à partir de l'équation de régression de la courbe a.

L'asymptote n'est atteinte qu'en mettant en œuvre un nombre important d'unités d'échantillonnage (1118 au total sur cet exemple). Le seuil des 50% des espèces totales est atteint au bout de 33 unités d'échantillonnage, et le seuil des 90% est atteint au bout de 548 unités d'échantillonnage.

I.2) Optimisation des coûts

I.2.1) D'autres familles difficiles d'identification à exclure ?

Les Staphylinidae ne sont pas les seules familles présentant des difficultés élevées d'identification. Il est également possible de citer les Mordellidae, Scraptiidae, Latridiidae, Ciidae, et bien d'autres encore. L'analyse de l'impact de la non-considération de ces familles sur les résultats d'études reste à évaluer. Il est probable que la non-prise en compte individuelle n'amène comme pour les Staphylinidae à aucune conséquence sur l'évaluation de paramètres environnementaux grossiers à large échelle. Mais pris de manière conjointe, il est possible que les résultats puissent changer. La quantité de données employée peut en effet changer les résultats d'étude dans 25% des cas (Parmain *et al.,* 2013 [1][1]).

I.2.2) Echelle européenne *vs* échelle locale

Le jeu de données que nous avons mobilisé est un agglomérat de différentes études locales. Chaque étude a été réalisée dans un but précis, et les variables environnementales récoltées l'ont été de manières différentes. De plus, toutes les variables n'étaient pas communes entre tous les jeux de données. Le lissage nécessaire pour pouvoir travailler avec des variables homogènes s'est fait 'par le bas'. Cela signifie qu'il est nécessaire de dégrader l'information des différentes sources au niveau le plus bas au sein de tous les jeux de données. Par exemple, si la variable « volume de bois mort » est disponible pour la totalité des jeux de données mais qu'elle est évaluée de manière précise dans un cas (volume mesuré de bois mort) et très grossière dans un autre (volume estimé, selon trois classes

[1] Le chiffre entre crochets fait référence aux articles définis dans le tableau 2.

'faible', 'moyen', 'fort'), il sera nécessaire de convertir l'information du volume en classe. Il y a donc une perte d'information liée à cette uniformisation. Il est possible que l'exclusion des Staphylinidae des jeux de données puisse avoir une influence significative sur les résultats d'études locales en relation avec des variables d'une plus grande finesse.

II) Perspectives

II.1) Portée de détection du piège à interception

Nous avons montré que les cortèges d'espèces obtenus entre deux pièges distants d'environ 20m sont significativement différents. Cette constatation avait également été effectuée par Sverdrup-Thygesson et Birkemoe (2009). Ceci plaide en faveur d'une influence importante des micro-conditions stationnelles pour expliquer les assemblages locaux des espèces. L'utilisation de plusieurs pièges par placette lorsque cela est possible permet de compenser cet effet. Pourtant, ce résultat plaide également en faveur de la nécessité de mettre en place un nombre de pièges élevé pour permettre de couvrir un grand nombre de conditions micro-stationnelles présentes au sein des forêts. Cette réflexion est particulièrement valable si le but est de contacter des espèces rares –dans le cadre de l'évaluation de l'état de conservation du milieu par exemple- généralement tributaires d'habitats particuliers et raréfiées dans les forêts exploitées.

II.2) Cas particulier des espèces rares

Il est important d'introduire la notion d'espèce spécialiste et/ou rare à ce stade du raisonnement. En effet, un écosystème qui verrait sa richesse spécifique augmenter suite à une perturbation non naturelle ne serait pas forcément en bon état de conservation. Il faut donc principalement prendre en compte les espèces spécialistes des écosystèmes concernés - si la richesse spécifique est utilisée comme indicateur du bon état de conservation de l'écosystème- même si elles y sont communes. Vient ensuite le cas particulier des espèces rares ou sur les listes rouges de conservation (red-listed). Ces espèces présentent des degrés de sensibilité différents à l'égard des activités humaines et ne sont parfois retrouvées que dans les zones non (ou peu) impactées par les activités humaines (Poulin *et al.,* 2008 ; Roberge *et al.,* 2008 ; Molina *et al.,* 2006).

Il existe deux façons de caractériser une espèce rare : (i) a priori (ii) a posteriori.

La caractérisation a priori va se baser sur la connaissance de la communauté des entomologistes, pratiquant des prospections à l'aide de méthodes diverses. C'est l'approche de la rareté telle qu'utilisée par Brustel (2001) pour les coléoptères saproxyliques ou par Pétillon *et al,* (2007) pour les araignées. Elle est dépendante des connaissances générales du groupe mais permet d'évaluer la rareté d'une espèce au niveau national. Cela permet la construction d'une base de données référençant les espèces, en indiquant leur degré de rareté. Suite à un échantillonnage, il sera aisé de déterminer le degré de rareté d'une espèce, en s'affranchissant des biais crées par l'échantillonnage.

La caractérisation a postériori se fait au vu des données récoltées. Elle est généralement basée sur la proportion d'individus que représente chaque espèce au sein du pool total d'espèces contactées (Gering *et al.,* 2003) mais peut également répondre à la définition des espèces qui n'ont été contactées qu'une seule fois sur l'ensemble du jeu de données (Novotny et Basset, 2000). Une

espèce pourra donc être rare dans un cas, et commune dans un autre, en fonction des aléas d'échantillonnage, et du milieu d'étude.

Une approche 'mixte' est proposée par Leroy *et al,* (2012). Leur méthode permet d'assigner une valeur de rareté à une espèce en fonction de son occurrence au sein des données étudiées, en prenant en compte les données précédentes de la même zone et des zones adjacentes. L'originalité de cette approche réside également dans le choix de l'échelle spatiale. Le degré de rareté peut être évalué au niveau local, régional ou national en fonction des objectifs recherchés, à condition de posséder des données sur l'ensemble de la zone considérée. Elle combine ainsi rareté a priori et a posteriori.

L'utilisation de la rareté des espèces est utile en biologie de la conservation. La présence de ces espèces au sein des milieux étudiés traduit généralement un bon état de conservation (Siitonen et Saaristo, 2000). Elles participent activement au bon fonctionnement de l'écosystème (Lyons *et al.,* 2005). Les espèces rares a priori sont généralement dépendantes de niveaux trophiques élevés, qui ne se retrouvent que peu ou pas dans les systèmes dégradés. En forêt, cela correspond aux forts volumes de bois morts et dendromicrohabitats, ainsi qu'à leur diversité (cf Chapitre III). Cependant, ce raisonnement n'est pas applicable à l'approche a posteriori de la rareté. On peut par exemple se retrouver dans un cas de figure de zone forestière en bon état de conservation, où des espèces dépendantes de hauts niveaux trophiques d'habitat vont être contactées en nombre, et ne pas être considérées en tant qu'espèces rares. Les espèces rares alors détectées pourront alors être des espèces 'touristes' qui n'ont aucune relation avec le milieu étudié, des espèces communes dépendantes de bois fraichement mort et ensoleillé (compartiment rare dans les stades terminaux de la sylvigenèse, mais commun dans les stades initiaux) des espèces difficilement détectables avec la méthodologie employée (Horak *et al.,* 2013) ou des espèces effectivement rares a priori et contactées en faible nombre.

L'approche de la rareté a posteriori seule n'est à mon sens pas compatible avec une approche de la conservation. En effet, les espèces spécialistes du milieu sont à privilégier pour la conservation, plutôt que les espèces peu échantillonnées pour d'autres raisons. De futures études devraient comparer les conclusions obtenues pour un même jeu de données comparant zone préservée et zone exploitée avec un focus sur les espèces rares en utilisant les deux méthodes de caractérisation.

II.3) Recherche d'espèces cibles

Actuellement, l'évaluation de la valeur patrimoniale des forêts (*i.e* de leur intérêt de conservation) s'effectue de plusieurs manières. L'une d'elles est l'utilisation des coléoptères saproxyliques comme groupe indicateur. Cette approche a été facilitée par les travaux de Brustel, (2001) qui a défini une liste de 300 espèces indicatrices de la valeur patrimoniale des forêts de France. Ces espèces sont donc prioritairement recherchées lorsque l'évaluation du milieu au moyen des coléoptères saproxyliques est menée. De manière standard, ces prospections sont conduites sur trois ans, avec un nombre variable des pièges à interception, en fonction des moyens alloués à l'étude (Nageleisen et Bouget, 2009). Ces espèces indicatrices de la qualité du milieu sont généralement des espèces rares. De par leur nature, elles vont être difficiles à contacter, et peuvent nécessiter la mise en place

de techniques dédiées (Gouix et Brustel, 2012). Dans ce cas précis, l'évaluation de la pression d'échantillonnage à fournir pour avoir 90% de chance de contacter l'espèce a été mené. Cette information est particulièrement utile pour le gestionnaire et le conservateur de la forêt. Une telle démarche entreprise à titre exploratoire pour les espèces indicatrices de la valeur patrimoniale des forêts a été menée (Annexe 2), et mérite d'être approfondie.

II.4) L'outil génétique, nouvel allié de l'entomologiste ?

La phase de laboratoire nécessaire à l'identification de chacun des individus à l'échelle de l'espèce est chronophage et demande une bonne connaissance de la taxinomie des groupes étudiés, ainsi que l'accès à de la bibliographie parfois rare. L'utilisation de moyens pour simplifier cette tâche a été envisagée (Sebek *et al.,* 2012).

Actuellement, les progrès des outils génétiques permettent de séquencer rapidement et à moindre coût du matériel biologique. Une technique en particulier permet d'obtenir une liste de 'code-barres' à partir d'un échantillon de milieu naturel (eau, terre) (Yu *et al.,* 2012). Les codes-barres obtenus correspondent à autant d'espèces qui étaient présente dans l'échantillon traité. Il est ainsi possible d'estimer la richesse spécifique des milieux échantillonnés par cette méthode. Cependant, les codes-barres seuls ne sont pas d'une grande utilité, puisqu'ils ne révèlent pas directement l'identité de l'espèce considérée. Il faut pour cela mener un travail de construction de bibliothèques de références, en effectuant la procédure de création de code barre pour des échantillons de référence. Une fois cette bibliothèque créée, les codes-barres issus des échantillons pourront être rattachés à des espèces. Les données générées par ce moyen permettent de s'affranchir de l'identification individuelle des spécimens. La création d'une bibliothèque de référence est actuellement en cours pour les coléoptères de France et d'Europe, avec un focus sur les espèces saproxyliques (Rougerie *et al., under review* ; Annexe 5).

Chapitre III :

Impacts locaux des éléments de la TTVB

Chapitre III : Impacts locaux des éléments de la TTVB

Ce chapitre se divise en deux parties. Nous explorons dans un premier temps l'effet des réserves forestières et des ilots de vieillissement sur la modification des caractéristiques de stocks de bois mort et dendromicrohabitats, et l'influence que cela a sur les assemblages de coléoptères saproxyliques. Dans un deuxième temps, l'évaluation de la contribution d'une structure non forestière de la TTVB à la conservation des coléoptères saproxyliques est menée.

Publications associées à ce chapitre: Articles **3** ; **4** ; **5** et **6** (cf Tableau 2).

Partie I : Réserves forestières et ilots de vieux bois

Les éléments forestiers de la TTVB sont constitués par les réserves forestières, les ilots de vieux bois et les arbres habitats. Le principe de fonctionnement écologique de ces mesures est lié à une gestion reposant sur la non-intervention, ou le retardement de la phase d'exploitation. Dans les zones laissées en libre évolution, la reprise du cycle sylvigénétique sera amorcée. Les phases terminales du cycle pourront alors s'effectuer, et les compartiments affectés par l'exploitation forestière se reconstituer. Dans les zones où le cycle d'exploitation est rallongé, la totalité des compartiments ne sera pas restaurée, car l'exploitation finale est maintenue. Cependant, certains compartiments comme le volume d'arbres de très gros diamètre ou une partie des dendromicrohabitats pourraient être positivement affectés.

L'identification des structures les plus favorables à la diversité des coléoptères saproxyliques semble dépendante des contextes considérés. En milieux boréaux, d'importants volumes de bois mort semblent être la clé de la conservation de la majorité des espèces (Lassauce *et al.,* 2011). Au contraire, en milieu tempéré, le volume de bois mort a une importance moindre par rapport aux dendromicrohabitats. La vitesse de restauration du milieu suite à l'exploitation du milieu a été évaluée dans plusieurs contextes, particulièrement au regard du compartiment des dendromicrohabitats (Larrieu, 2014). Il est primordial de caractériser précisément quelles vont être les structures clés pour la conservation de la biodiversité des coléoptères saproxyliques.

Nous avons entrepris à travers trois études la caractérisation (i) des compartiments bois mort et dendromicrohabitats les plus favorables aux coléoptères saproxyliques ; (ii) de l'évolution de leur quantité en fonction de la durée de non exploitation ou d'allongement du cycle sylvicole ; (iii) de la réponse des assemblages de coléoptères saproxyliques à ces modifications de milieu.

Nous avons mis en évidence l'impact positif des méthodes d'arrêt d'exploitation pour la reconstitution des stocks et des structures caractéristiques des stades avancés de la sylvigenèse (bois mort, dendromicrohabitats). En parallèle, les cortèges d'espèces saproxyliques ne répondent que faiblement à cette modification de milieu sur le court terme. Différentes hypothèses sont avancées pour expliquer cette constatation. Enfin, le rallongement de cycle d'exploitation tout en maintenant les activités sylvicoles ne semble avoir d'effet que pour les caractéristiques structurelles du milieu

liées aux arbres vivants. Aucun impact positif ou négatif n'a été observé concernant les coléoptères saproxyliques.

De nombreux paramètres restent encore mal connus comme par exemple l'impact des ilots de vieillissement ou de plus longues durées de non exploitation sur la modification du milieu et la réaction des communautés de coléoptères saproxyliques.

Animal Conservation **17** (2014) 342–353 © 2014 The Zoological Society of London Received 06 May 2013; accepted 28 November 2013

Article 5: Does a set aside conservation strategy help the restoration of old-growth attributes and the recolonization of saproxylic beetles?

C. Bouget*, G. Parmain*,°,*, O. Gilg¤, T. Noblecourt°, B. Nusillard*, Y. Paillet*, C. Pernot*, L. Larrieu**, F. Gosselin***

* National Research Institute of Science and Technology for Environment and Agriculture. (IRSTEA), 'Forest ecosystems' Research Unit, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France (christophe.bouget@irstea.fr; guilhem.parmain@irstea.fr; benoit.nusillard@irstea.fr; yoan.paillet@irstea.fr; coryse.pernot@irstea.fr; frederic.gosselin@irstea.fr). ** INRA, INPT/ENSAT/EIPURPAN, UMR 1201 Dynafor, F-31326 Castanet-Tolosan, France and CNPF-IDF, 7 chemin de la Lacade, F-31320 Auzeville Tolosane, France. laurent.larrieu@toulouse.inra.fr ° National Laboratory of Forest Entomology, National Forest Office (ONF), F-11500 Quillan, France *** National Museum of Natural History, Natural Patrimony Department, 36 rue Geoffroy St Hilaire, CP 41 75 231 PARIS CEDEX 05, France. ¤ Réserves Naturelles de France, 6bis, rue de la Gouge. CS60100 - 21803 Quétigny, France olivier.gilg@espaces-naturels.fr

Abstract

The decline of many saproxylic species results from the decrease in old-growth structures in European harvested forests. Among conservation tools, protected reserves withdrawn from regular harvesting and extended rotations have been employed to restore old-growth attributes in structurally simplified managed forests, even if the effects of such management actions on forest habitats and biodiversity remain largely unknown.

In this study, we compared structural stand features and saproxylic beetle assemblages in two stand classes - recently harvested stands and long-established reserves, where less or more than thirty years had elapsed since last harvest. Habitat and saproxylic beetle data were collected according to standardized protocols in 153 plots in seven lowland deciduous forests.

Tangible contrasts in stand features were found between long-established reserves and recently-harvested plots. Indeed, most higher-value densities and volumes were found in unharvested areas. The difference was weaker for microhabitat-bearing tree density than for deadwood; some deadwood features, such as volume of large downed and standing deadwood showed a very pronounced difference, thus indicating a marked deleterious effect of forest harvesting on these elements. Deadwood diversity, on the other hand, was only slightly affected and the level of stand openness did not change.

The response of saproxylic beetles to delayed harvesting was weaker than the structural changes in deadwood features. Nevertheless, long-established reserves showed higher species richness and slightly but significantly dissimilar species assemblages than recently-harvested plots. Indeed even if only some guilds weakly increased in non-harvested plots, harvesting classes significantly affected the abundance of a quarter of the species tested.

Our results tend to question measures such as rotating and temporarily ageing patches. We argue in favor of permanent strict fixed-location reserves. Future work should examine how stands

recover old-growth forest attributes and how the associated saproxylic fauna colonises in the long-term.

KeyWords: Delayed harvesting; forest reserves; temperate deciduous forests; insect biodiversity; deadwood; tree microhabitats

Introduction

European forest dynamics has been deeply affected by forestry and forest fragmentation for millennia (Peterken, 1996). Stand composition and structure have been greatly simplified by harvesting and other uses, even in remote areas. Several studies demonstrated the negative effects of conventional management practices on old-growth structures (e.g. Burascano et al., 2013; Green and Peterken 1997; Lombardi et al. 2008). Structural simplification has been shown to result in the decline of many associated saproxylic populations, but the issue has received more attention in North America and northern Europe than in central and southern Europe (e.g. Martikainen et al., 2000; Grove, 2002).

In forests subjected to structural simplification through harvesting, strategies to restore old-growth attributes may involve (i) setting aside forest plots, (ii) extended rotations, (iii) retention of structural features at the time of harvest and (Keeton, 2006) (iv) man-made restoration of structural elements (Martikainen et al., 2000). In the last 20 years, there has been an increasing focus on systematic conservation planning, i.e. how to select protected areas in a way that captures biodiversity as efficiently as possible (e.g. Margules and Pressey, 2000). Protected forests include different protection categories and surface areas (Schmitt et al., 2009), and they are described worldwide in countless ways. Areas 'left for natural dynamics' can be found in several protection categories often as (so-called) strict forest reserves, where neither silvicultural intervention nor any other avoidable human impacts are allowed, but other denominations abound: wilderness areas, areas withdrawn from regular management, abandoned, unharvested, set-aside forest areas or unmanaged core areas in national parks. Among passive restoration strategies (Bauhus et al., 2009), small-scale management tools such as delaying harvesting, leaving unharvested patches or preserving habitat trees (Lachat and Bütler, 2009) have been employed to increase the number of old-growth structures in forests (Bauhus et al., 2009). Other examples include woodland-key-habitats, green-tree retention patches left in clearcuts as short-term refuges or lifeboats for many organisms during the regeneration phase in Scandinavia and North America (e.g. Vanha-Majamaa and Jalonen, 2001, Aubry et al., 1999), ageing or old-growth patches kept as portions of management units in France (Lassauce et al., 2013). Despite an increase in the number of empirical studies concerning the effects of forest abandonment on species diversity (see Paillet et al., 2010), the relative efficiency of each management strategy in supporting biodiversity remains unknown. When harvesting activities are delayed for several decades, natural forest dynamics may bring about structural changes that restore old-growth attributes, depending on site potential (Vandekerkhove et al., 2009): larger trees, heterogeneous vertical and horizontal structure with greater variations in tree

size, age, spacing and species composition, increased supplies of deadwood, more large snags and fallen trees, multiple canopy layers, changes in disturbance regime, canopy gaps and understory patchiness. These structural changes have been recorded in several case studies (e.g. Lassauce et al., 2012 and 2013, Sitzia et al., 2012) and may impact biodiversity.

In this study, we compared the habitat parameters and the diversity of saproxylic beetles (i.e. abundance, species richness and composition) in set-aside and harvested areas in seven lowland deciduous French forests. The issues were addressed in two steps: (i) How were saproxylic habitat parameters, such as the diversity and density of deadwood and tree microhabitats, affected in long-established set-aside plots compared with recently harvested plots? (ii) Did saproxylic beetle assemblages (incl. rare species) respond to these habitat changes?

Material and methods

Study areas

The plots were located in seven lowland beech (Fagus sylvatica L.) and oak (Quercus robur L. and Q. petraea (Mattus.) Liebl.) forests (Tab. 1) in the Atlantic or Continental biogeographic domain. Each forest was several hundred kilometers from the others: one in western France (Chize), three in eastern France (Auberive, Citeaux, Combe-Lavaux), one in central France (Troncais) and two in northern France (Rambouillet, Fontainebleau). The plots in each forest were several hundred meters apart. A design of 153 plots was set up in managed stands (98) and in recently- (16) or long-established (39) forest reserves. Managed forests were coppice-with-standards under conversion to high forest (33), even-aged (54) or uneven-aged (11) high forests (see Supplementary material). All plots were located in mature stands before regeneration felling or final cut. Last harvests consist of thinning operations in even-aged high forests and single tree removals in coppice-with-standards stands under conversion and uneven-aged high forests. The time elapsed from last harvest was postulated for each plot based on management plans, reports or information from local managers. Unlike Christensen et al. (2005), we did not derive the number of years since last harvest from the official establishment date of the reserves since these do not necessarily coincide. Because the time since last harvest was not precisely known in several cases, we classified the plots into two harvesting classes based on the best estimate of the length of time without harvesting or removal of trees and deadwood (Tab. 1): 'recently-harvested' (R-HAR<30 years ago, n=114), including harvested plots (n=98) and recently-established reserves (n=16); or long-established reserves (L-UNH>30 yrs, n=39), including old (>30 yrs and <100yrs, n=30) and very old reserves (>100 yrs, n=9). Very old reserves were found in the Fontainebleau state forest only. We collected environmental and entomological data following standardized protocols.

Beetle sampling and identification, species characterization

Flying saproxylic beetles were sampled by two cross-vane flight interception traps (PolytrapTM) per plot, set about 20 m from each other, for a total number of 306 traps. The unbaited traps were suspended roughly 1.5 m above ground. Active insects were collected from April to August during one year. For each species in all the taxa from the ±50 families recorded, we

characterized degree of geographic rarity in France according to the FRISBEE database (http://frisbee.nogent.cemagref.fr/index.php/en/) and distinguished common (abundant and/or widely distributed) and rare (not abundant and only locally distributed) species. All species were assigned to one saproxylic trophic group, but only the four main guilds were studied (xylomycetophagous, xylophagous, saproxylophagous, zoophagous).

Stand and deadwood variables

We used a combination of fixed-area and fixed-angle techniques to estimate (i) wood volumes for live trees, snags, logs and stumps, and (ii) the basal area of live trees on 0.15ha (Fontainebleau, Auberive, Chize, Citeaux, Combe-Lavaux) or 0.30ha (Rambouillet, Troncais) plots. We set a minimum diameter of 7.5 cm for live trees, snags and logs.

Four variables were used to describe the deadwood: tree species, diameter (6 classes: 5,10-15, 20-25, 30-40, 50-65, >70 cm), position (log, snag, stump), decay stage (9 classes adapted from Sippola et al. (1998) and Larjavaara and Muller-Landau (2010) and crossing 3 classes of remaining bark cover [from 95% of the stem still covered by attached bark to missing bark over the whole stem] and 3 classes of inner wood hardness assessed by “knife penetration test” [from hard outer wood to deeply disintegrated and soft inner wood]). A deadwood diversity index was calculated as the number of observed deadwood types, i.e. the number of combinations of the above four variables (tree species*diameter class*decay class*position), as suggested by Siitonen et al. (2000). The volume of live trees was calculated using wood volume tables based on the dbh variable, and used to estimate the deadwood volume ratio (=dead wood/(live + dead wood)), accounting for site productivity (Hahn and Christensen, 2004). Based on the deadwood surveys, we selected seven deadwood variables for analysis: (i) deadwood volume, (ii) deadwood volume ratio, (iii) number of deadwood types, (iv) standing deadwood volume, (v) large standing deadwood (diameter>40cm) volume, (vi) downed deadwood volume, and (vii) large downed deadwood (diameter>40cm) volume. The thresholds defining large deadwood, large and very large trees were inspired by results in Nilsson et al. (2003) and Larrieu and Cabanettes (2012).

The basal area of large trees (67.5<dbh ≤87.5 cm) and very large trees (dbh>87.5 cm) were measured on 0.15-0.3ha plots; the density of large trees was also inventoried in 1-ha circular plots. Tree microhabitat densities were inventoried during leaf-burst in 1-ha circular plots centered around the two flight traps. We recorded seven microhabitat types borne by live trees (Larrieu and Cabanettes, 2012): (i) "empty" cavities, (ii) cavities with mould, (iii) fruiting bodies of saproxylic fungi, (iv) sap runs, (v) dead branches, (vi) tree crown deadwood, and (vii) missing bark (i.e. hard patches of wood with no bark > 600 cm² (see Tab. 2 for further details on predictors). Microhabitats other than crown deadwood were only recorded when visible on the trunk beneath and within the tree crown. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type. The total density of microhabitats, the number of microhabitat types (among the 7 observed types) and the individual densities of four microhabitat types (“empty” and mould cavities pooled, dead branches and tree crown deadwood pooled, sporocarps of saproxylic fungi, and sap runs) were considered for analysis. Stand openness was assessed as the total proportion of open areas (clearings, edges, stand surface

with a well-developed herb layer composed of flowering plants) in a 1ha plot. For further details on how the environmental variables were measured, see Bouget et al. (2013).

Data analysis

Our main objectives were to compare (i) stand structural characteristics and (ii) saproxylic beetle assemblages in the two stand classes (R-HAR and L-UNH) based on the amount of time elapsed since last harvest. Because the same set of environmental variables was used for both traps in the same plot, the catches of the two traps were combined prior to analyses carried out at the plot level.

The differences in mean values of structural stand features between recently-harvested and long-established reserves were analyzed with a Generalized Gaussian or Poisson Linear Mixed Model where "forest" was a spatially-implicit random effect on the intercept (lmer function in lme4 R-package).

To rank the effect of the harvesting variable among structural predictors of variations in common or rare species richness, we assessed the multi-model-averaged estimates (Burnham and Anderson 2002) determining the response of species richness to stand features. Since co-linearity among predictor variables may lead to unreliable parameter estimates, we implemented the strategy suggested by Zuur et al. (2010) to address multi-colinearity before model averaging. We sequentially dropped the covariate with the highest variance inflation factor (VIF), then recalculated the VIFs and repeated this process until all VIFs were below a pre-selected threshold (Zuur et al. (2010) suggest a cutoff at 3). We used the "vif.mer" function to calculate VIFs for linear mixed-effects models built using the lmer function in the "lme4" package (Tab. 2). Since the relationship between species richness and deadwood volumes is better described by semi-log models (Martikainen et al., 2000), we used (log x+1)-transformed values for deadwood volumes. The selected variables with VIF<3 were: harvesting class, openness, basal area of very large trees (dbh>87.5cm), large tree 1ha-density, density of sap-run-bearing trees, of fungus-bearing trees, of cavity-bearing trees, of crown deadwood-bearing trees, number of microhabitat types, total deadwood volume, deadwood ratio, log10 (large downed deadwood volume), log10 (large standing deadwood volume) . For each response variable, we generated the null model and generalized linear mixed models (Poisson error structure) with all the combinations of two explanatory variables. Using the differences in the Akaike information criterion (AICc) scores between each model and the best model (ΔAICc) as well as the Akaike weights for each model, we calculated the model-averaged estimates., Only significant variables ($p<0.10$ across all the models) were displayed (lme4, MuMIn, arm; R-packages).

To rank the effect of the harvesting variable among structural predictors on variations in species composition (including singletons), we performed a Canonical Analysis of Principal Coordinates (vegan R-package, CAP, Anderson and Willis 2003). Based on Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, since co-linearity among predictor variables is not considered to be a problem in CAP. We calculated total constrained inertia, the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance (permutation tests - 100 runs), and the relative contribution of each set of variables (deadwood, microhabitat, stand, forest, harvesting

class) to constrained inertia. In addition, we used a pairwise ANOSIM procedure based on Jaccard distance matrices to test for differences in assemblage composition among predefined groups with spatially-constrained permutation tests (Clarke, 1993); the grouping factor was the harvesting treatment, and the spatial constraint the forest.

We also used a generalized linear mixed model, with a spatially-implicit variable (forest) as a random factor on the intercept and a Poisson error distribution, to analyze the differences between the two harvesting classes in i) mean abundance and richness per plot of rare or common species and trophic groups, and ii) mean abundance of selected species (more than 20 individuals caught and occurring in at least 10 out of the 153 plots in our dataset). Since we found a close correlation between total abundance and the number of beetle species recorded on a plot, we used the number of individuals as a covariate in the richness models (Gotelli and Colwell, 2001) to separate the effects on the number of individuals from species effects. To analyze differences in occurrence per plot of selected beetle species between the two harvesting classes, we used a Generalized Linear Mixed Model with a Binomial error structure and “forest” as a spatial random effect (lmer function in lme4 R-package). In order to quantify the magnitude of significant differences between R-HAR and L-UNH treatments, we computed an index by dividing model estimates for each of the harvesting treatments (estimate L-UNH/ estimate R-HAR) with “forest” as a random factor.

All analyses were conducted using R v2.12.0. All R-packages used are available online at http://cran.r-project.org/web/packages/available_packages_by_name.html. The “vif.mer” function is available online at https://github.com/aufrank/R-hacks/blob/master/mer-utils.R.

Results

Overall, the compiled dataset included 99,383 individuals in 476 beetle species (25 taxa identified at the genus level only), among which 377 common, 69 rare (15% of the total number) and 30 species with an undefined rarity status were recorded.

1. Habitat parameters in recently-harvested plots vs long-established reserves

Significant differences in stand features (deadwood, micro-habitat, large trees, openness) were measured between long-established reserves (L-UNH) and recently-harvested plots (R-HAR) (Tab. 2). Values for deadwood (deadwood volume, deadwood ratio, number of deadwood types, downed deadwood volume, large standing deadwood volume, standing deadwood volume, large standing deadwood volume), and microhabitats (density of microhabitat-bearing trees, number of microhabitat types, density of cavity-bearing trees, density of deadwood-bearing trees, density of fungus-bearing trees) and large tree characteristics (basal area of large trees and very large trees, density of large trees) were always considerably higher in long-established reserves than in recently-harvested plots. Deadwood diversity was only slightly, though significantly, higher in long-established reserves. Only the density of sap-run-bearing trees and openness values remained significantly unaffected by the harvesting class.

The magnitude of the differences between R-HAR and L-UNH plots was even more pronounced with respect to certain deadwood features. These differences were characterized by a high relative increase from R-HAR to L-UNH i.e. the ratio dividing estimates in L-UNH by R-HAR for four variables: large downed deadwood volume (estimate ratio=8.97); large standing deadwood volume (estimate ratio =8.79); standing deadwood volume (estimate ratio =4.84); basal area of very large trees (estimate ratio =4.80). This indicates a strong negative effect of forest harvesting on those attributes. According to the estimate ratio, the differences measured between long-established reserves and recently-harvested plots were even more pronounced for large deadwood volumes than for large tree characteristics. Microhabitat features were not as impacted as were deadwood and stand features by the harvesting class (Tab. 2).

2. Saproxylic beetle diversity in recently-harvested plots vs long-established reserves

Species composition

Variations in total inertia of saproxylic beetle assemblages were explained by geographical (35.0%), deadwood (9.0%), microhabitats (8.8%) and stand structural characteristics (7.0%) (Tab. 3). Only openness, microhabitat diversity, deadwood ratio and deadwood diversity had a significant ($p<0.05$), though marginal, contribution to variations in species composition. As along with the density of fungus-bearing trees and large standing deadwood volume, the class of time elapsed since harvesting showed a non-significant trend ($p<0.1$), accounting for only 1.7% of the constrained inertia. A spatially-constrained ANOSIM test also showed slightly, but significantly, dissimilar species assemblages between the harvesting classes (1000 permutations, R: 0.168; Significance: 0.002).

Species richness

The class of time elapsed since harvesting was not a key variable for saproxylic beetle species richness; it ranked fifth in explanatory value among the twelve structural stand features, and was only slightly significant (Tab. 4). Long-established reserves however showed a higher saproxylic beetle species richness than recently-harvested plots (Tab. 4). The best models for both rare and common species were the number of deadwood types and openness, and the best for common species was deadwood volume ratio.

Guild composition

The abundance of common and xylophagous species was significantly lower in long-established reserves than in recently-harvested plots. Zoophagous species abundance was not sensitive to the harvesting class. In contrast, mycophagous, saproxylophagous and rare species were more abundant in long-established reserves. The number of mycophagous, zoophagous, and common species per plot, after accounting for abundance, was slightly, but significantly, higher in long-established reserves. For saproxylophagous, xylophagous and rare species, no significant difference in species richness was observed between harvesting classes (Tab. 5).

Individual species responses

At the individual species level, about 25% (n = 39.) of the tested species had a significant response in abundance to the harvesting class. The same proportion of significantly responding species occurred in both harvesting classes: half of the species were significantly more abundant in recently-harvested plots, and half were significantly more abundant in long-established reserves. Two rare taxa were included among the species responding positively to long-established reserves (none were found in recently-harvested plots; Tab. 6).

Discussion

Changes in stand structure induced by non-harvesting

In long-established reserves (i.e. plots set-aside for at least 30 years) originating from managed stands, we measured tangible contrasts in stand characteristics compared with recently-harvested plots. Indeed, most of the stand characteristics we studied displayed higher volume and density values in long-established set-asides than in recently harvested areas.

More than 30 years without harvesting allowed the deadwood volumes to increase significantly. Vandekerkhove et al. (2005) already showed that deadwood can accumulate quite fast in forest reserves, especially in terms of density. In abandoned beech forests in Germany, Meyer and Schmidt (2011) indicated a rather fast relative increase in deadwood volume: total deadwood doubled in about 9 years (standing deadwood in 7 years). Such figures are probably dependent on dominant tree species, soil fertility and the silvicultural stage of the stand at the time it was set aside. Several other studies found a similarly significant increase in deadwood volume in long-unharvested stands compared with managed ones (Kirby et al., 1991; Sippola et al., 1998; Motta et al., 2010; Calamini et al., 2011), or at least for coarse woody debris (Boncina, 2000; Marage and Lemperiere, 2005; Sitzia et al., 2012). Timonen et al. (2011) also demonstrated that deadwood volumes are higher in woodland key habitats than in managed stands.

However, we showed that deadwood diversity only increased slightly in long-established reserves (partly due to the lack of large-diameter logs in late decay stages). Nonetheless, in the data compiled by Timonen et al., (2011), deadwood diversity was much higher in woodland key habitats compared with managed stands, probably partly due to an initial selection effect, i.e. deadwood in the selected plots when they were selected as set asides or as key habitats.

The difference between long-established reserves and recently-managed plots may be more pronounced with respect to certain deadwood qualities, as suggested by Siitonen et al. (2000). In their Finnish study in spruce forests, large dead coniferous and deciduous trees were respectively 25 and 35 times more abundant on average, in unharvested plots than in recently-harvested stands. Accordingly, we found a strong impact of harvesting on large dead wood (downed and standing), with a ninefold increase in large deadwood when harvesting is delayed for at least 30 years. This increase in large deadwood was twice as high as for total deadwood volume. Boncina (2000) and Meyer and Schmidt (2011) also found a rapid accumulation of standing deadwood from unmanaged to managed stands.

Nonetheless, more deadwood was found in longer-established beech reserves (Christensen et al., 2005), and in 60-year-old over-mature French coppices compared to 20-year-old mature coppice (Lassauce et al., 2012). Vandekerkhove et al. (2009) argued that full natural restoration of deadwood characteristics (with virgin forests in Central Europe as a reference) may be quite long. Furthermore, Larrieu et al. (2012) showed that a 50-year period of non-intervention was too short to develop complete stand maturity in beech-fir stands, even in highly productivity contexts.

Like Bauhus et al. (2009), we were able to detect a list of structural elements (deadwood, microhabitats, large trees) which become significantly more frequent in unharvested stands. We also showed, in accordance with the results simulated by Ball et al. (1999), that the increase in microhabitat-bearing tree density was weaker than the increase in deadwood density. Reaching high levels of microhabitat density requires time, since the probability of microhabitat occurrence or the number of microhabitat types increases with tree diameter (e.g. Larrieu et al., 2012). In a simulation model, Ranius et al. (2009) pointed out the importance of tree age for cavity formation on trees (see also empirical data in Gibbons et al., 2010). Furthermore, Fan et al. (2003 and 2005) showed a higher frequency of cavity trees in 120-year-old forests than in younger stands, and in old-growth than in managed stands (like Bauhus et al., 2009). In our results, a slightly higher density of cavity-bearing trees was measured in long-established reserves than in recently-harvested plots.

Across our sampling design, long-established reserves and recently-harvested forests did not differ in terms of stand openness, since the stands were too young to be significantly impacted by canopy gap dynamics. Gap dynamics is known to increase average sun exposure in old-growth forests compared with managed stands (Rugani et al., 2013), and open forest habitats are required by a large number of specialized saproxylic species (Vodka et al. 2009).

Effect of non-harvesting on saproxylic beetle assemblages

In our study, the effect of non-harvesting on biodiversity was slightly significant. The class of time elapsed since harvesting seemed to be important for 25% of the tested species, but was not as important a variable as structural parameters for saproxylic beetle assemblages in our data. Some guilds and groups were positively influenced by non-harvesting (mycophagous abundance and richness, saproxylophagous and rare species abundance), but the relationship was weak and clearly had less impact than deadwood features (see Tab. 2 and Tab. 4). Many saproxylic species may simply require a small amount of dead wood that is also available in managed forests. Or structural changes in stand characteristics may occur more quickly than the response of saproxylic organisms. Delayed responses by saproxylic beetle communities may be due to the limited ability, at least for old-growth forest specialists, to colonize favourable substrates (dispersal, habitat detection…) and their density-dependence in the colonization process. Local assemblages may be deeply affected over the long term by historical deadwood supplies (Hanski and Ovaskainen, 2002). Furthermore, population levels must reach minimum thresholds for species to be detected. This interpretation is reflected in our study: the two most typically influential variables for saproxylic beetle richness – deadwood diversity and openness – did not respond strongly to more than 30 years without harvesting. Yet, deadwood diversity has been recognized as a key factor for saproxylic beetle diversity in temperate deciduous forests (Bouget et al., 2013) and other studies based on similar time frames have demonstrated significant responses of saproxylic beetle diversity to setting aside forest areas (Timonen et al., 2011;

Lassauce et al., 2013). However, Horák et al. (2012) raised the question of the status of the rare species pool, deeply affected by commercial forestry in European multi-secular managed forests. In our study (Tab. 5), rare species were more abundant (but not more species-rich) in forest reserves than in managed plots (in agreement with previous results by Lassauce et al., 2013 and Hardersen, 2003 in Germany). We therefore hypothesize (i) that set-aside areas may act as incubators for rare species found in neighboring managed areas, or (ii) that forest management reduces the amount of habitats available to rare species and therefore their populations, without leading them to disappear or (iii) that most rare species have disappeared and only populations of a few surviving species increase with the amount of dead wood. To address these questions, it would be helpful to use very old reserves as references for species distribution and abundance. Considering the short set aside period in our study, saproxylic beetle assemblages were probably strongly influenced by both initial forest conditions (pre-existing large trees, beetle assemblages…) and the spatial isolation of the plots. The comparison between managed stands and set-asides should be deepened and a long-term monitoring strategy put in place (Djupström et al., 2008).

Implications for forest management

Extended rotations, harvesting delays and reserves as conservation tools

In French forests, temporarily setting aside overmature stands before final harvesting, i.e. creating ageing and rotating islands (Lassauce et al. 2013), is one of the management tools proposed to maintain saproxylic biodiversity associated with old successional stages. This approach aims to conciliate both timber production and biodiversity conservation goals. Larger trees generally have higher economic value while older stands have higher ecological value. We have shown that even a short delay in harvesting (minimum 30 years) induced significant changes in habitat conditions for saproxylic beetles, but only slightly affected saproxylic beetle assemblages. Further studies with longer harvesting delays would be necessary to analyse biodiversity responses. If longer-term habitat continuity is necessary for saproxylic beetle conservation, our results suggest that definitive strict fixed-location reserves should be favored over rotating and temporary set-asides. Moreover, the efficiency of ageing patches as temporary ecological sinks or sources has yet to be properly investigated.

Limits of management relinquishment and non-intervention: towards active restoration techniques?

Passive self-restoration of old-growth features through the abandonment of forest activities in harvestable deciduous stands takes time, at least for some features crucial for species conservation (large deadwood, tree microhabitats…). Therefore, complementary active restoration techniques may be suggested to enhance the recruitment and accumulation of new substrates in conservation areas. Keeton (2006) showed that, in conventional silvicultural systems, active restoration is more successful in creating old-growth features than is delaying harvesting. For instance, standing dead trees, large downed deadwood and tree cavities can be artificially generated using cost-effective techniques like girdling trees, felling or pulling down large trees to be left on the forest floor and mechanically damaging tree trunks (with or without fungus inoculation). Costlier

experiments with extreme habitat restoration have even been carried out in Italy (e.g. Cavalli and Donini, 2005). Active restoration requires an in-depth understanding of natural habitats to avoid structures inappropriate to local biodiversity; Jonsell et al. (2004), for example, have underlined the differences between man-made and natural deadwood habitats. In any case, since most endangered saproxylic species have limited dispersal ability (e.g. Buse, 2012), the proper spatial distribution of created substrates is a prerequisite for effective restoration programs. The ecological impacts of active restoration techniques on biodiversity, but also on potential bark beetle outbreaks, should be monitored (Toivanen and Kotiaho, 2010). Thus said, active techniques should at least be considered when the restoration process must achieve the desired forest state within a relatively short time or when the species at stake are threatened by external factors.

Conclusions

Our results did not strongly support recommendations about extended rotations and reserve conservation in favor of saproxylic biodiversity. The rationale behind it would probably benefit from further studies in very old forest reserves, although they are scarce in Western Europe. In one of the study forests (Fontainebleau), despite a limited and unbalanced sampling design, we divided the class of long-established reserves into old (>30 yrs, n=3) and very old (>100 yrs, n=9) reserves. From our exploratory analysis, the deadwood volume and diversity, the total beetle species richness, the rare species richness or abundance were not significantly higher in the older class. This trend deserves to be assessed by other case studies.

Forest areas left unharvested for more than 30 years show an accumulation of old-growth structures related to deadwood volumes and microhabitat diversity, but not deep changes in saproxylic beetle diversity. Restoring the old-growth-dependent community as a whole seems even slower than restoring these structural features. As suggested by Paillet et al. (2010), future work should examine the temporal effect of delayed harvesting at multiple time points on the same study area in order to evaluate, using a regression approach with the detailed time elapsed since harvesting, (i) how stands recover old-growth forest attributes and (ii) how the associated saproxylic fauna colonize these set-asides in the long-term.

Acknowledgements

We are grateful to A. Lassauce, C. Moliard (Irstea), T. Barnouin, F. Soldati (ONF), N. Debaive (RNF) and all the local forest managers for field and laboratory work. We are indebted to Vicki Moore who reviewed the English manuscript, and to three anonymous reviewers whose constructive comments on an earlier version improved the manuscript. This research was granted by the French ministry in charge of the Ecology through the "Biodiversité, Gestion Forestière et Politiques Publiques" (BGF) program (convention RESINE CVOJ 000 150, convention 10-MBGD-BGF-1-CVS-092, n°CHORUS 2100 214 651) and the National Forestry Board ("Office National des Forets", convention ONF-Cemagref, Action 5, 2008). This work was also partly funded by the French Environment and Energy Management Agency (ADEME).

References

Anderson, M.J. & Willis, T.J. (2003). Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84: 511-524.

Aubry, K.B. Amaranthus, M.P. Halpern, C.B. White, J.D. Woodard, B.L. Peterson, C.E. Lagoudakis, C.A. & Horton, A.J. (1999). Evaluating the Effects of Varying Levels and Patterns of Green-tree Retention: Experimental Design of the DEMO Study. North. Sci. 73: 12-26.

Ball, J.P. Lindenmayer, D.B. & Possingham, H.P. (1999). A tree hollow dynamics simulation model. For. Ecol. Manag. 123: 179-184.

Bauhus, J. Puettmann, K. & Messier, C. (2009). Silviculture for old-growth attributes. For. Ecol. Manag. 258: 525-537.

Boncina, A. (2000). Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia. Global Ecol. Biogeogr. 9: 201–211

Bouget, C. Larrieu, L. Parmain, G. & Nusillard, B. (2013) In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodiv. Conserv. 22:2111–2130

Burnham, K.P. & Anderson, D.R. (2002). Model selection and multimodel inference, Second edition. Springer-Verlag, New York, New York, USA.

Burrascano, S. Keeton, W.S. Sabatini, F.M. & Blasi, C. (2013). Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. For. Ecol. Manag. 291: 458-479.

Buse, J. (2012). “Ghosts of the past”: flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. J. Ins. Cons. 16: 93-102

Calamini, G. Maltoni, A. Travaglini, D. Iovino, F. Nicolaci, A. Menguzzato, G. Corona, P. Ferrari, B. Di Santo, D. Chirici, G. & Lombardi, F. (2011). Stand structure attributes in potential Old-Growth Forests in the Apennines, Italy. Ital. For. Mont. 66: 365–381.

Cavalli, R. & Donini, F. (2005). Possible management actions to increase the amount of dead and marcescent wood p.45-48, In Mason, F. Nardi, G. & Tisato, M. (eds). Deadwood: a key to biodiversity. p. 100, Mantova (Italy).

Christensen, M. Hahn, K. Mountford, E.P. Ódor, P. Standovár, T. Rozenbergar, D. Diaci, J. Wijdeven, S. Meyer, P. Winter, S. & Vrska, T. (2005), Deadwood in European beech (Fagus sylvatica) forest reserves. For. Ecol. Manag. 210:267–282.

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. Austr. Jour. of Ecol. 18: 117-143.

Djupström, L.B. Weslien, J. & Schroeder, L.M. (2008). Deadwood and saproxylic beetles in set-aside and non set-aside forests in a boreal region. For. Ecol. Manag. 255: 3340-3350.

Fan, Z.F. Larsen, D.R. Shifley, S.R. & Thompson, F.R. (2003). Estimating cavity tree abundance by stand age and basal area, Missouri, USA. For. Ecol. Manag. 179: 231-242.

Fan, Z. Shifley, S.R. Spetich, M.A. Thompson, F.R. & Larsen, D.R. (2005). Abundance and Size Distribution of Cavity Trees in Second-Growth and Old-Growth Central Hardwood Forests. North. Jour. of App. For. 22: 162-169.

Gibbons, P. McElhinny, C. & Lindenmayer, D.B. (2010). What strategies are effective for perpetuating structures provided by old trees in harvested forests? A case study on trees with hollows in south-eastern Australia. For. Ecol. Manag. 260: 975-982.

Gotelli, N. & Colwell, R. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters. 4: 379-391.

Green, P. & Peterken, G.F. (1997). Variation in the amount of deadwood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. For. Ecol. Manag. 98: 229-238.

Grove, S.J. (2002). Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics. 33: 1-23.

Hahn, K. & Christensen, M. (2004). Dead wood in European Forest Reserves - a reference for forest management. p. 181-191. In: Marchetti M. (ed.) Monitoring and indicators of forest biodiversity in Europe - From ideas to operationality, EFI Proceedings No. 51

Hanski, I. & Ovaskainen, O. (2002). Extinction Debt at Extinction Threshold. Cons. Biol. 16: 666-673.

Harderssen, S. (2003). Two lowland beech-oak forest areas abandoned for more than 30 years: what do bird and beetle communities tell us? p.33-36. In: Mason, F. Nardi, G. & Tisato, M. (eds.), Proceedings of the International Symposium: Deadwood: a key to biodiversity, Mantova, May 29th -31st 2003. Sherwood 95, Suppl. 2

Horák, J. Chobot, K. & Horáková, J. (2012) Hanging on by the tips of the tarsi: A review of the plight of the critically endangered saproxylic beetle in European forests. Jour. Nat. Conserv. 20, 101-108.

Jonsell, M. Nittérus, K. & Stighäll, K. (2004) Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biol. Conserv. 118: 163–173.

Keeton, W.S. (2006). Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. For. Ecol. Manag. 235: 129-142.

Kirby, K.J. Webster, S.D. & Antczak, A. (1991). Effects of forest management on stand structure and the quantity of fallen deadwood: some British and Polish examples. For. Ecol. Manag. 43: 167–174.

Lachat, T. & Bütler, R. (2009). Identifying conservation and restoration priorities for saproxylic and old-growth forest species: a case study in Switzerland. Env. Manag. 44: 105–118.

Larjavaara, M. & Muller-Landau, H.C. (2010). Comparison of decay classification, knife test and two penetrometers for estimating wood density of coarse woody debris. Can J Forest Res 40: 2313-2321.

Larrieu, L. & Cabanettes, A. (2012). Tree species and girth are key determinants for diversity and abundance of tree microhabitats in sub-natural montane beech-fir forests. Can J Forest Res 42: 1433–1445

Larrieu, L. Cabanettes, A. & Delarue, A. (2012). Impact of silviculture on deadwood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. Europ. Jour. For. Res. 131: 773-786.

Lassauce, A. Anselle, P. Lieutier, F. & Bouget, C. (2012). Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: A case study in French deciduous forests. For. Ecol. Manag. 266: 273-285.

Lassauce, A. Larrieu, L. Paillet, Y. Lieutier, F. & Bouget, C. (2013). The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation length in French oak high forest. Ins. Conserv. Div. 6: 396–410

Lombardi, F. Lasserre, B. Tognetti, R. & Marchetti, M. (2008) Deadwood in relation to stand management and forest type in Central Apennines (Molise, Italy). Ecosyst. 11: 882–894.

Marage, D. & Lemperiere, G. (2005). The management of snags: a comparison in managed and unmanaged ancient forests of the Southern French Alps. Ann. For. Sci. 62: 135–142.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning; Nature (London) 405: 243–253.

Martikainen, P. Siitonen, J. Punttila, P. Kaila, L. Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol. Conserv. 94: 199-209.

Meyer, P. & Schmidt, M. (2011). Accumulation of deadwood in abandoned beech (Fagus sylvatica L.) forests in northwestern Germany. For. Ecol. Manag. 261: 343-352.

Motta, R. Berretti, R. Castagneri, D. Lingua, E. Nola, P. & Vacchiano, G. (2010) Stand and coarse woody debris dynamics in subalpine Norway spruce forests withdrawn from regular management. Ann. For. Sci. 67: 1-8.

Nilsson, S.G. Niklasson, M. Hedin, J. Aronsson, G. Gutowski, J.M. Linder, P. Ljungberg, H. Mikusinski, G. & Ranius, T. (2003). Erratum to ‘‘Densities of large living and dead trees in old-growth temperate and boreal forests’’. For. Ecol. Manag. 178: 355-370.

Paillet, Y. Bergès, L. Hjältén, J. Odor, P. Avon, C. Bernhardt-Römermann, M. Bijlsma, R.-J. de Bruyn, L. Fuhr, M. Grandin, U. Kana, R. Lundin, L. Luque, S. Magura, T. Matesanz, S. Mézaros, I. Sebastia, M.-T. Schmidt, W. Standovar, T. Tothmérész, B. Uotila, A. Valladares, F. Vellak, K. & Virtanen, R. (2010). Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. Conserv. Biol. 24: 101-112.

Peterken, G.F. (1996). Natural Woodland. Ecology and Conservation in Northern Temperate Regions. Cambridge University Press, Cambridge.

Ranius,T. Niklasson, M. & Berg, N. (2009). Development of tree hollows in pedunculate oak (Quercus robur). For. Ecol. Manag. 257: 303-310.

Rugani, T. Diaci, J. & Hladnik, D. (2013) Gap Dynamics and Structure of Two Old-Growth Beech Forest Remnants in Slovenia. PLoS ONE 8: e52641. doi:10.1371/journal.pone.0052641.

Schmitt, C. Burgess, N. Coad, L. Belokurov, A. Besançon, C. Boisrobert, L. Campbell, A. Fish, L. Gliddon, D. Humphries, K. Kapos, V. Loucks, C. Lysenko, I. Miles, L. Mills, C. Minnemeyer, S. Pistorius, T. Ravilious, C. Steininger, M. & Winkel, G. (2009). Global analysis of the protection status of the world's forests. Biol. Conserv. 142: 2122–2130

Siitonen, J. Martikainen, P. Punttila, P. & Rauh J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For. Ecol. Manag. 128: 211–225.

Sippola, A.-L. Siitonen, J. & Kallio, R. (1998). Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. Scan. Jour. For. Res. 13: 204-214.

Sitzia, T. Trentanovi, G. Dainese, M. Gobbo, G. Lingua, E. & Sommacal, M. (2012). Stand structure and plant species diversity in managed and abandoned silver fir mature woodlands. For. Ecol. Manag. 270: 232–238.

Timonen, J. Gustafsson, L. Kotiaho, J.S. & Mönkkönen, M. (2011). Are woodland key habitats biodiversity hotspots in boreal forests? CEE review 09-020 (SR81). Collaboration for Environmental Evidence: www.environmentalevidence.org/SR81.html.

Toivanen, T. & Kotiaho, J.S. (2010). The preferences of saproxylic beetle species for different deadwood types created in forest restoration treatments. Can. J. For. Res. 40: 445–464.

Vandekerkhove, K. De Keersmaeker, L. Menke, N. Meyer, P. & Verschelde, P. (2009). When nature takes over from man: Deadwood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. For. Ecol. Manag. 258: 425-435.

Vandekerkhove, K. De Keersmaeker, L. Baeté, H. & Walleyn, R. (2005). Spontaneous re-establishment of natural structure and related biodiversity in a previously managed beech forest in Belgium after 20 years of non intervention For. Snow Landsc. Res. 79: 145–156.

Vanha-Majamaa, I. & Jalonen, J. (2001). Green Tree Retention in Fennoscandian Forestry. Scan. Jour. For. Res. 16: 79-90.

Vodka, S. Konvicka, M. & Cizek, L. (2009). Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. Jour. Ins. Conserv. 13: 553-562.

Zuur, A.F. Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. Meth. Ecol. and Evol. 1: 3-14.

Table. 1: Sampling design layout. Among L-UNH long-established reserves, old (>30 yrs) and very old reserves (>100 yrs) were not tested separately due to the small number of replicates available in the latter category. Managed plots and recently-established reserves are grouped in R-HAR. Sampling year between brackets.

	beech			oak			Total
	R-HAR <30 yrs	L-UNH > 30yrs		R-HAR <30 yrs	L-UNH > 30yrs		
		30-100 yrs	> 100yrs		30-100 yrs	> 100yrs	
Auberive [2009]	11	4		7	2		24
Chize [2010]	10	2		12			24
Citeaux [2010]				6	6		12
Combe-Lavaux [2010]	3	2		1	2		8
Fontainebleau [2008]	5	3	9	7			24
Rambouillet [2007]				24	6		30
Troncais [2009]				28	3		31
Total	29	11	9	85	19	0	153

Table 2: Effect of the harvesting class on stand characteristics (deadwood, micro-habitat, large trees, openness). Stands were classified as recently-managed (R-HAR <30 yrs ago) or long-established reserves (L-UNH > 30yrs ago). Differences in stand features between the two harvesting classes were tested with a linear mixed model (NS= not significant; * 0.05>p>0.01; ** 0.05>p>0.001; *** p<0.001). Ratio = ratio dividing estimates of L-UNH by R-HAR (see Material and Methods). (s.e. between parentheses)

	Factor	Detail	signif	Est R-HAR	Est L-UNH	ratio	Error distribution family
Stand features	Basal area of large trees	Basal area of large trees in a 0.3ha plot (67.5<dbh ≤87.5 cm) (m²/ha)	***	2.957 (1.579)	7.198 (1.663)	2.43	gaussian
	Basal area of very large trees	Basal area of the very large trees in a 0.3ha plot (dbh>87.5 cm) (m²/ha)	***	0.501 (0.591)	2.405 (0.628)	4.80	gaussian
	Density of large trees	Number of large trees in a 1ha plot (dbh>67. 5cm)	***	1.389 (0.487)	2.116 (0.487)	1.52	poisson
	Openness	Proportion in cumulative area of open areas (clearings, edges, areas with a well developed herb layer composed of flowering plants) (%) in a circular 1ha plot	NS	12.490 (5.188)	11.667 (5.962)		gaussian
MH features	Density of microhabitat-bearing trees	Total density of microhabitat-bearing trees in a 1ha plot	***	2.647 (0.129)	3.046 (0.131)	1.15	poisson
	Number of microhabitat types	Number of microhabitat types in a 1ha plot	**	1.468 (0.061)	1.702 (0.070)	1.16	poisson
	Density of cavity-bearing trees	Density of cavity-bearing trees in a 1ha plot: "empty" cavities with an entrance above 3 cm in width, woodpecker breeding and feeding holes, deep cavities formed between roots, cavities with mould with an entrance above 10 cm in width	***	1.620 (0.093)	2.208 (0.098)	1.36	poisson
	Density of fungus-bearing trees	Density of fungus-bearing trees in a 1ha plot: fruiting bodies of tough or pulpy saproxylic fungi, >5cm in diameter,	***	0.397 (0.203)	0.458 (0.208)	1.15	poisson
	Density of deadwood-bearing trees	Density of deadwood-bearing trees a 1ha plot: crown deadwood in (large dead branches > 20 cm in diameter	**	1.624	1.824 (0.278)	1.12	poisson

		and > 1 m in length, crown deadwood volume > 20% of the total crown wood volume)		(0.276)			
	Density of sap-run-bearing trees	Density of sap-run-bearing trees: sap runs > 10 cm in length in a 1ha plot	NS	-1.142 (0.327)	-1.359 (0.394)		poisson
DW features	Deadwood volume	Total volume of deadwood in a 0.3ha plot (m3/ha)	***	22.677 (9.539)	79.976 (10.992)	3.53	gaussian
	Deadwood ratio	Volume ratio=deadwood /(Live trees+deadwood)	***	0.099 (0.025)	0.225 (0.030)	2.27	gaussian
	Large downed deadwood volume	Volume of large downed deadwood (>40 cm in diameter) in a 0.3ha plot (m3/ha)	***	3.052 (4.029)	27.387 (4.875)	8.97	gaussian
	Large standing deadwood volume	Volume of large standing deadwood (> 40 cm in diameter)) in a 0.3ha plot (m3/ha)	***	2.123 (3.067)	18.658 (3.701)	8.79	gaussian
	Standing deadwood volume	Volume of standing deadwood (>10 cm in diameter) in a 0.3ha plot (m3/ha)	***	4.529 (2.811)	21.910 (3.572)	4.84	gaussian
	Downed deadwood volume	Volume of downed deadwood (>10 cm in diameter) in a 0.3ha plot (m3/ha)	***	16.791 (7.487)	57.373 (8.684)	3.42	gaussian
	Number of deadwood types	Nb deadwood types (tree species*diameter*decay*position)	**	2.400 (0.243)	2.559 (0.245)	1.07	poisson

Table 3. Ranked effect of the harvesting class among structural and spatial predictors on variations in species composition. Canonical Analysis of Principal coordinates (CAP) used to partition the variation in the response species-plot matrix with respect to the combination of explanatory stand features (deadwood, microhabitat, large trees, openness); %CI: relative contribution to constrained inertia

Significance of marginal contribution to inertia: ° 0.1>p>0.05; * 0.05>p>0.01; ** 0.01>p>0.001

	Predictors	Cumulated marginal inertia	%IC
Spatial	Forest**	7.348	34.97%
Set-aside	Harvesting class°	0.357	1.699%
Stand	Basal area of large trees, Basal area of very large trees, Density of large trees, Openness**	1.475	7.019%
MH	Total density of microhabitats, Number of microhabitat types*, Density of cavity-bearing trees, of fungus-bearing trees°, of deadwood-bearing trees, of sap-run-bearing trees	1.863	8.866%
DW	log10 (Total volume deadwood), Deadwood ratio*, log10 (large downed deadwood volume), log10 (large standing deadwood volume)°, log10 (downed deadwood volume), log10 (standing deadwood volume), Number of deadwood types*	1.899	9.041%

Table 4. Ranked effect of the harvesting class among structural predictors on variations in species richness. Multi-model averaged estimates for structural stand features (deadwood, microhabitats, large trees, openness) and harvesting class determining the response of saproxylic beetle species richness (rare, common). Relative importance is the weight of evidence for each parameter across all the best models combining several variables (mixed-effect models, with forest as a random effect). Only significant variables (° 0.1>p>0.05; * 0.05>p>0.01; ** 0.01>p>0.001; *** p<0.001) were selected.

species richness	variable	Variable Model-averaged estimate (significance)	Relative contribution	Best models (DeltaAICc<3)	
Rare	1.Number of deadwood types	1.48 ***	0.93	divDW+open	AICc=596.8
	2. Openness	0.81 **	0.65		
Common	1.Openness	10.02 ***	1.00		
	2.Deadwood ratio	6.53 ***	0.51		
	3.Number of deadwood types	10.81 ***	0.45		
	4. Harvesting class	3.92 °	0.01	open+ratio	AICc=1166.7
	5. Density of cavity-bearing trees	3.70 °	0.01	divDW +open	AICc=1167.0
	6. log10 (Volume of large downed deadwood)	3.70 °	0.01		

Table 5. Values of the estimates (s.e. between parentheses) from generalized linear mixed effect models with a Poisson error distribution for abundance and richness of ecological groups of saproxylic beetles species in 'recently-harvested (R-HAR<30 years ago) or 'long-established reserves' (L-UNH>30years ago). Probability (p) of a significant difference between mean values is indicated by: NS= not significant. *p<0.05. **p<0.01.***p<0.001.

We used the abundance of a covariate in species richness models.

		Abundance			Species richness		
		estimate R-HAR	estimate L-UNH		estimate R-HAR	estimate L-UNH	
Feeding guilds	Mycophagous	4.066 (0.306)	4.201 (0.306)	***	2.25 (0.099)	2.395 (0.106)	*
	Saproxylophagous	2.345 (0.340)	2.533 (0.341)	***	1.339 (0.172)	1.415 (0.180)	NS
	Zoophagous	4.029 (0.154)	4.038 (0.155)	NS	2.099 (0.119)	2.233 (0.124)	*
	Xylophagous	5.056 (0.457)	4.745 (0.457)	***	2.65 (0.077)	2.601 (0.084)	NS
Rarity groups	Common	5.773 (0.341)	5.572 (0.341)	***	3.682 (0.001)	3.776 (0.001)	**
	Rare	2.073 (0.431)	2.27 (0.432)	***	0.744 (0.184)	0.919 (0.1985)	NS
	Total	5.859 (0.326)	5.672 (0.326)	***	3.786 (0.001)	3.889 (0.001)	***

Table 6. Difference in abundance per plot of selected species between 'recently-harvested' (R-HAR<30 years ago) or 'long-established reserves' (L-UNH>30years ago) plots. Only significant differences are shown (p-value <0.001 after a Bonferroni correction for 150 tests). Only species sampled in at least 10 plots and with more than 20 individuals were analyzed, with generalized linear mixed-effect models and a Binomial error distribution; 'forest' was a random factor. Bold indicates significant in occurrence. (*) indicates rare species.

abundance > in R-HAR	abundance > in L-UNH
Ampedus quercicola	Anaspis flava
Anaglyptus mysticus	Anaspis melanopa
Anostirus purpureus	Cis boleti
Aulonothroscus brevicollis	Clerus mutillarius
Cyclorhipidion bodoanus	Corticeus unicolor
Ernoporicus fagi	Cryptarcha undata
Hemicoelus fulvicornis	Dasytes plumbeus
Hylecoetus dermestoides	Dryocoetes villosus
Leiopus femoratus	Hylis olexai
Litargus connexus	Mycetochara maura
Megatoma undata	Mycetophagus ater(*)
Phymatodes testaceus	Oxylaemus cylindricus
Platycerus caraboides	Paromalus parallelepipedus
Stenocorus meridianus	Ptilinus fuscus(*)
Taphrorychus bicolor	Rhagium bifasciatum
Tetratoma ancora	Scolytus rugulosus
Vincenzellus ruficollis	Thanasimus formicarius
Xyleborinus saxesenii	Tritoma bipustulata
Xyleborus dispar	Trypodendron signatum
	Xyleborus dryographus

Synthèse de l'article 5

cle	Problématiques	Résultats Habitat	Résultats coléoptères saproxyliques	Points discutés	Questions soulevées	Perspectives d'étude	Conclusions
	(1) Quelle est l'influence de la durée de non-exploitation sur les caractéristiques d'habitat des saproxyliques (volume et diversité de bois mort, dendromicohabitats)? (2) Quelle est la réponse des assemblages d'espèces de coléoptères saproxyliques (incluant les espèces rares) à ces changements?	<u>Eléments plus abondants en zones non exploitées depuis + de 30ans:</u> Surface des gros arbres (67.5<DBH<87.5cm) à l'hectare; Surface des très gros arbres (DBH>87.5cm) à l'hectare; Nombre de gros arbres (DBH>67.5cm) à l'hectare; Densité d'arbres porteurs de microhabitats à l'hectare; Diversité en dendromicrohabitats à l'hectare; Densité d'arbres à cavité à l'hectare; Densité d'arbres avec champignons saproxyliques à l'hectare; Densité d'arbres avec du bois mort dans le houppier; Volume total de bois mort à l'hectare; Ratio bois vivant/bois mort; Volume de gros bois mort (>40cm de diamètre) au sol à l'hectare; Volume de gros bois mort (>40cm de diamètre) debout à l'hectare; Volume de bois mort (diamètre >10cm) debout à l'hectare; Volume de bois mort (diamètre >10cm) au sol à l'hectare; Diversité de bois morts. <u>Pas de différences:</u> Ouverture du milieu, Densité d'arbres porteurs de coulées de sève à l'hectare.	<u>Déterminants des assemblages</u>: Spatial (Forêt) (35%); bois mort (toutes caractéristiques réunies) (9%); dendromicrohabitats (toutes caractéristiques réunies) (8.8%); caractéristiques placette (toutes caractéristiques réunies) (7%). Assemblages d'espèces entre placettes exploitées depuis moins de 30 ans et placettes non exploitées depuis plus de 30ans différents. <u>Déterminants richesse spécifique</u>: *Espèces rares*: diversité du bois mort; Ouverture du milieu. *Espèces communes*: Ouverture du milieu, ratio bois mort/bois total; diversité bois mort; duré de non exploitation (forte pvalue); densité d'arbres à cavités (forte pvalue);log10 volume de gros bois au sol (pvalue 0.1). <u>Variation richesse spécifique</u>: *Espèces rares*: pas de différence. *Espèces communes:* plus d'espèces en zone non-exploitée. *Prédateurs:* plus d'espèces dans les zones non exploitées. *Mycophages:* plus d'espèces dans les zones non exploitées. <u>Variation abondance</u>*: Espèces rares*: plus d'individus dans les zones non-exploitées. *Espèces communes*: Plus d'individus dans les zones exploitées. *Mycophages*: lus d'abondance dans les zones non exploitées. *Saproxylophages:* plus d'individus dans les zones non exploitées. *Xylophages:* plus d'individus dans les zones exploitées. <u>Réponse individuelle des espèces</u>: Autant d'espèces ont une abondance plus importante dans les zones exploitées que dans les zones non-exploitées. Deux espèces rares parmi les espèces ayant une abondance plus importantes en zone non exploitée. Aucune espèce rare avec une abondance plus importante en zone exploitée.	<u>Habitat</u>: Accumulation rapide du bois mort dans les zones non exploitées. Mais faible augmentation de la diversité. Compartiments particulièrement impactés (gros bois morts). L'augmentation du nombre de dendromicrohabitats est plus faible que l'augmentation des volumes de bois mort. <u>Espèces</u>: capacités de colonisation, besoins particuliers en habitat. Cas particulier des espèces rares	<u>Espèces</u>: La non-réponse de certains groupes peut s'expliquer par le faible besoin potentiel en volume bois mort, ce volume pouvant être disponible en zones exploitées. Une autre explication serait le délai de réponse plus grand pour les espèces que pour l'habitat; cela peut venir (pour les spécialistes des stades avancés de la sylvigenèse) de capacités de dispersion limitées, de détection d'habitat. <u>Habitat:</u> rôle d'incubateurs des zones non exploitées? Niveaux de populations des espèces rares réduits par l'exploitation forestières, ne permettant plus leur détectabilité? La plupart des espèces rares ont disparu des forêts exploitées il y à longtemps, seules quelques espèces restent et leurs niveaux de population augmentent avec l'augmentation de la qualité/quantité d'habitat?	Anciennes réserves comme références pour la richesse en espèces et l'abondance de ces espèces. Besoin d'études sur le long terme. Meilleure prise en compte des effets de restauration active de l'habitat sur les espèces. Colonisation des substrats régénérés naturellement au cours du temps.	Pas de grand soutien de l'étude à l'extension de rotation ni aux réserves forestières.

Tableau 3 : Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? Problématiques, résultats, éléments particuliers discutés, nouvelles problématiques posée, perspectives d'études à envisager et conclusions principales de l'article.

Biodivers Conserv (**2013**) 22:2111–2130 DOI 10.1007/s10531-013-0531-3. Received: 4 March 2013 / Accepted: 9 July 2013 / Published online: 23 July 2013

Article 6: In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests

Bouget, C.(1)*, Larrieu, L.(2), Nusillard, B.(1), Parmain, G.(1,3,4)

(1) National Research Institute of Science and Technology for Environment and Agriculture (Irstea), 'Forest ecosystems' Research Unit, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France christophe.bouget@irstea.fr, tel. 00-33-2-38-95-05-42, fax. 00-33-2-38-95-03-59 guilhem.parmain@irstea.fr benoit.nusillard@irstea.fr (2) INRA, INPT/ENSAT/EIPURPAN, UMR 1201 Dynafor, F-31326 Castanet-Tolosan, France and Centre Régional de la Propriété Forestière de Midi-Pyrénées, 7 chemin de la Lacade, F-31320 Auzeville Tolosane, France. Laurent.Larrieu@toulouse.inra.fr (3) National Laboratory of Forest Entomology, National Forest Office (ONF), 2 rue Charles Péguy, F-11500 Quillan, France (4) National Museum of Natural History, Natural Patrimony Department, 36 rue Geoffroy St Hilaire, CP 41 75 231 PARIS CEDEX 05, France

* corresponding author

Abstract

Deadwood-associated species are increasingly targeted in forest biodiversity conservation. In order to improve structural biodiversity indicators and sustainable management guidelines, we need to elucidate ecological and anthropogenic drivers of saproxylic diversity. Herein we aim to disentangle the effects of local habitat attributes which presumably drive saproxylic beetle communities in temperate lowland deciduous forests.

We collected data on saproxylic beetles in 104 oak and 49 beech stands in seven French lowland forests and used deadwood, microhabitat and stand features (large trees, openness) as predictor variables to describe local forest conditions.

Deadwood diversity and stand openness were consistent key habitat features for species richness and composition in deciduous forests. Large downed deadwood volume was a significant predictor of beetle species richness in oak forests only. In addition, the density of cavity- and fungus-bearing trees had weak but significant effects.

We recommend that forest managers favor the local diversification of deadwood types, especially the number of combinations of deadwood positions and tree species, the retention of large downed deadwood and microhabitat-bearing trees in order to maximize the saproxylic beetle diversity at the stand scale in deciduous forests.

To improve our understanding of deadwood-biodiversity relationships, further research should be based on targeted surveys on species-microhabitat relationships and should investigate

the role of landscape-scale deadwood resources and of historical gaps in continuity of key features availability at the local scale.

Key-words: Microhabitat; Deadwood; Forest management; Biodiversity indicator; Oak; Beech

Introduction

Deadwood is a key component of forest ecosystems that is among the most severely affected by management in many landscapes (Fridman and Waldheim, 2000) and has become a focal conservation target in sustainable management. Since deadwood is one of the most species-rich components in forest ecosystems (Grove, 2002a), saproxylic species have become increasingly targeted in biodiversity conservation (Stokland et al., 2012). Deadwood has often been used as a structural indicator for naturalness and biodiversity and can provide information on the intensity of past human disturbances and degree of proximity to old-growth conditions (Larsson, 2001). To help define ecologically-meaningful saproxylic-friendly practices for forest managers, we need to unravel the relative importance of ecological and anthropogenic drivers on saproxylic diversity.

Multiple factors play pivotal roles in predicting both the number and distribution of saproxylic species. Species assemblage composition may result from (i) macro-ecological features (distribution area, climate), (ii) environmental characteristics at the landscape scale and at the local scale, (iii) historical events (past disruption of substrate availability, local extinctions) and (iv) species interactions (competition, predation, interactive succession) (Stokland et al., 2012). Forestry practices act at the stand and the landscape scales. Therefore the understanding of variables driving biodiversity at the stand scale seems important to improve ecological sustainability of forestry.

Beetles are an important functional (Cobb et al., 2010) and numerical (20% of all saproxylic species, just after the fungi; Stokland et al., 2004) component of saproxylic biodiversity. Since beetles belong to relatively well-known taxonomic groups, and since most species are highly sensitive to environmental changes, have specific habitat demands and can be trapped relatively easily, they are both logistically and ecologically suitable as response indicators (Siitonen, 2001).

At the local (stand) scale, habitat quality for saproxylic beetles is related to abiotic conditions (e.g. moisture and temperature conditions related to canopy closure) and available resources. Resources not only include deadwood substrates, but also more cryptic biological legacies such as microhabitats (e.g. cavities, crown deadwood), mostly found in large-diameter live trees (Larrieu and Cabanettes, 2012; Winter and Möller, 2008). Density and/or diversity of resources may underlie the resource-biodiversity relationship. Forest stands with a wider range of resources (resource range hypothesis) and/or a higher density of substrates (resource concentration hypothesis) may be able to support a larger number of species due to demographic, stochastic and dispersal processes affecting local population dynamics (Päivinen et al., 2003). Several studies have demonstrated a positive significant correlation between the local amount of deadwood and saproxylic beetle species richness (see Grove, 2002a). Nevertheless, in a meta-analysis of available European data, Lassauce et al. (2011) found only a weak relationship between deadwood volume and species richness in temperate forests. Moreover, several studies have shown the diversity of deadwood types, rather than mere deadwood quantity, to be a critical environmental variable for saproxylic beetles (e.g. Brin et al., 2009; Stokland et al., 2004).

During the last few decades, research on saproxylic beetle habitat associations has been common in Scandinavia (Stokland et al., 2012), but has received less attention in central, western and southern Europe. By expanding this research to oak and beech forests, the two main deciduous forest types in Europe, we aimed to better understand the surrogacy patterns and environment-biodiversity relationships found there and to determine (i) relevant structural indicators of saproxylic beetle diversity and (ii) improved guidelines for sustainable forest management. We here mainly intended (i) to disentangle the effects of local habitat attributes (abiotic conditions, density or diversity of resources) which presumably drive saproxylic beetle communities in deciduous forests, and (ii) check whether key habitat features for saproxylic beetles are consistent over oak and beech forests.

Material and methods

Study areas

We collected environmental and entomological data using standardized protocols on 153 plots in seven lowland deciduous forests (Tab. 1), distant of several hundred kilometers from each other: one forest in western France (Chize), three in eastern France (Auberive, Citeaux, Combe-Lavaux), one in central France (Troncais) and two in northern France (Rambouillet, Fontainebleau).

Two forest types were distinguished - oak and beech - according to the dominant tree species in terms of basal area. All the beech stands were associated with oak stands in the vicinity. Highland beech forests have been studied in a companion study. Inside each forest, plots were distant of hundreds of meters from each other and half of the plots were located in protected forest reserves (except in the Rambouillet and the Troncais forest, where only 20% and 10% were in reserve stands, respectively).

Beetle sampling and identification, species characterization

Flying saproxylic beetles were sampled with two cross-vane flight interception traps (Polytrap^{TM}) per plot, set about 20 m from each other, for a total number of 306 traps. The traps were suspended roughly 1.5 m above the ground. Active insects were collected from April to August, during one year only. The following saproxylic taxa were not identified at the species level in at least one of the seven forests and therefore removed from the compiled dataset: Cryptophagidae, Ptiliidae, Staphylinidae incl. Scaphidiinae and Pselaphinae. For the other taxa, we characterized each species' degree of geographic rarity in France according to the FRISBEE database (Bouget et al. 2010) and distinguished common (abundant and/or widely distributed) and rare (not abundant and only locally distributed) species of conservation concern for specific analyses.

Live tree and deadwood measurements

Stands were surveyed to obtain estimates of wood volumes for live trees, snags, logs and stumps and the basal area of live trees. Each plot, centered in the middle of both traps, was approximately 0.3 ha in size. We used a combination of sampling methods: fixed-angle relascope or circular plots for live trees; circular plots for stumps, large snags and large logs; line intersect sampling for small logs. We took into account minimum diameters of 7.5 cm for live trees, snags and logs. Four variables were used to describe deadwood: tree species, diameter (6 classes from 5 to >70 cm), decay stage (9 classes created by crossing 3 classes of remaining bark cover and 3 classes of inner wood hardness assessed by "knife penetration test"; Larjavaara and Muller-Landau, 2010), and position (downed, standing, stump). An index of deadwood diversity was calculated as the number of observed deadwood types, i.e. the number of combinations of the above four variables (tree species*diameter class*decay class*position), as suggested by Siitonen et al. (2000). We also figured out a Shannon deadwood diversity index (Dodelin et al., 2004), accounting for the individual density (i.e. its number of pieces), and not only the occurrence, of each deadwood type. Based on these

surveys, seven deadwood variables were considered for analysis (Tab. 1): (i) total volume, (ii) volume ratio, (iii) number of deadwood types, (iv) volume of standing deadwood, (v) volume of large standing deadwood (>40 cm in mid-diameter), (vi) volume of downed deadwood, (vii) volume of large downed deadwood (>40 cm in mid-diameter).

The basal area of very large and largest live trees was calculated for each 0.3-ha plot. The thresholds defining large trees were given by Grove (2002b), Larrieu and Cabanettes (2012) and Nilsson et al. (2002).

Very large live trees (67.5<dbh ≤87.5 cm) and tree microhabitats were inventoried during leaf-out in 1-ha circular plots centered around the two traps. We recorded seven microhabitat types borne by live trees: (i) "empty" cavities, (ii) cavities with mould, (iii) fruiting bodies of saproxylic fungi, (iv) sap runs, (v) dead branches, (vi) tree crown deadwood, (vii) missing bark (i.e. hard patches of wood with no bark > 600 cm²). Microhabitats other than crown deadwood were only recorded when visible on the trunk beneath and within the tree crown. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type. The total density of microhabitat-bearing trees, the number of microhabitat types and the individual densities of four microhabitat types (i)“empty” and mould cavities, ii) sporocarps of saproxylic fungi, iii) dead branches and tree crown deadwood and iv) sap runs) were considered for analysis. Stand openness was defined as the total proportion of open areas in a 1-ha plot.

Data analysis

We used deadwood, microhabitat and stand features as predictor variables to describe forest conditions (Tab. 1), and species richness of *rare* and *common* species and species composition (incl. singletons) as response variables to describe beetle assemblages. All analyses were conducted on oak and beech datasets with R software v. 2.12.0. Since the same set of environmental variables measured within the 0.3- and 1-ha plots was used for both traps in the same plot, the catches of these two traps were combined prior to analyses carried out at the *plot* level.

To rank the effects of environmental variables on variations in species composition, we performed a Canonical Analysis of Principal Coordinates (*vegan* R-package, CAP, Anderson and Willis 2003). From Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, since co-linearity among predictor variables is not considered to be a problem in CAP (Anderson and Willis 2003). We calculated total constrained inertia, the constrained

inertia which was not explained by spatial factors only (NSCI), the total (intrinsic + co-explained) inertia explained by each variable (after partialling out the geographical "*forest*" effect), the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance by means of permutation tests (100 runs), and the relative contribution of each variable to NSCI.

We assessed the multi-model-averaged estimates (Burnham and Anderson 2002) determining the response of species richness to stand features. The most parsimonious model had the lowest Akaike information criterion (AICc, Burnham and Anderson 2002). For each response variable, we generated the null model and models with all the valid combinations of two explanatory variables. We calculated the differences in the AICc scores between each model and the best model (ΔAICc) as well as the Akaike weights for each model. All models with ΔAICc < 2 were used in order to figure out the model-averaged estimates weighted by the model weights. Only significant variables ($p<0.05$ across all the models) were selected; their relative contribution, i.e. their weight of evidence across all the models, was indicated (*lme4*, *MuMIn*, *arm* R-packages). Since co-linearity among predictor variables may lead to unreliable parameter estimates, we conducted the strategy suggested by Zuur et al. (2010) for addressing the multicolinearity problem before model averaging. We sequentially dropped the covariate with the highest variance inflation factor (VIF), then recalculated the VIF and repeated this process until all VIFs were below a pre-selected threshold (Zuur et al. (2010) suggest a cutoff of 3). The VIF represents the proportion of variance in one predictor explained by all the other predictors in the model ; a VIF = 1 indicates no co-linearity, whereas increasingly higher values suggest increasing multicolinearity. We used the "vif.mer" function (Frank 2011) to calculate VIFs for linear mixed effects models built using the lmer function in the "lme4" package (Tab. 2). Since the relationship between species richness and deadwood volumes is better described by semi-log models (Martikainen et al., 2000), we used (log x+1) transformed values for deadwood volumes. The effect on species richness of local deadwood diversity assessed by the simple index (number of deadwood types) or the Shannon index (Shannon diversity index of deadwood types, taking the local density of each deadwood type into account, using its number of pieces) was compared using AICc values of each mixed model (with forest as a random factor).

Significant relationships in generalized linear models were searched for breakpoints in species accumulation rates. Estimates of breakpoints were calculated by recursive partitioning by means of maximally selected two-sample statistics (Hothorn et al., 2006). Only primary and significant ($p<0.001$) breakpoints are reported here. Based on 5,000 bootstrap samples, 80% confidence intervals (to define ranges more tightly than 95% CI) were calculated for all breakpoints

(*party* and *boot* R-packages). In comparison with other models used in the study, this method does not allow to take the spatial structure of the data (at least forest location) into account.

The diversity effect was partitioned into its four basic dimensions included in the deadwood diversity index (diameter class, decay class, tree species, position). We analysed whether any of these dimensions have an outstanding importance on species richness, by comparing AICc values of linear mixed models (with forest as a random factor) including all combinations of the 4 deadwood dimensions.

The response to stand openness of the abundance of selected beetle species (caught in more than 10 individuals occurring in more than 10% samples) was analyzed using a Generalized Linear Mixed Model with a Poisson error distribution, and "forest" as a spatial random effect (lmer function in lme4 R-package).

Results

Overall, the compiled dataset included 99 383 individuals and 478 saproxylic beetle species, among which 377 common, 70 rare (15% of the total number) and 31 undefined species were recorded. On average per plot, rare species represented about 6% of all species and 6% of all individuals. The mean numbers of common and rare species per plot were greater in the oak than in the beech plots (49.7+/-1.7 *vs* 38.1+/-1.9 and 3.5+/-0.2 *vs* 1.9+/-0.1, respectively). Significant differences in several explanatory stand features were measured between oak and beech plots (Tab. 1).

Response of species composition to stand features

Many factors were used to describe the saproxylic environment (deadwood, microhabitats, large trees, stand openness) in order to identify the main local factors driving saproxylic beetle diversity. In oak and beech data, environmental and spatial factors respectively accounted for 45% and 52% of variation in species composition. 31% and 23% of the constrained inertia was explained by the intrinsic site effect in oak and beech data.

In oak and beech forests, the openness, the microhabitat diversity, the deadwood diversity and the basal area of very large trees made significant total contributions (marginal and joined) to inertia (Tab. 3). In the oak forests, microhabitat density also provided a significant total contribution.

In the beech forests, significant total contributions were also provided by all the other deadwood descriptors (total volume, ratio, volumes of standing, large standing, downed, large downed deadwood), the density of very large trees at the 1-ha scale and the basal area of the largest trees. In oak, two environmental variables (deadwood diversity and stand openness) had a significant marginal contribution to inertia but only explained 3.5 and 3.9% of the non-spatial constrained inertia, respectively. In beech data, although a larger proportion of the inertia was explained by the environmental predictors than in oak data, none of the tested environmental predictors made a significant intrinsic contribution to inertia. In beech and oak forests, the density of cavity-, fungus-, deadwood-, sap-run-bearing trees did not explain variations in species composition.

Response of species richness to stand features

From multi-model averaged estimates (Tab. 4), the stand openness was the main predictor of richness of common beetle species in oak and beech plots. The deadwood diversity and the density of fungus-bearing trees had the highest positive impacts on rare species richness in oak and beech forests, respectively. The more open the forest and the higher the local number of deadwood types, the higher the number of common species per plot in beech and oak forests, and the number of rare species in oak stands. In oak stands, the number of common species also significantly increased with the volume of all downed deadwood (the second best predictor after openness), and to a lesser extent, with the volume of large downed deadwood, and with the density of fungus- and cavity-bearing trees. Overall, the influential stand features were only partially identical for rare and common species. The influence of the total volume of deadwood on the number of species was not tested, since it was collinear with other predictors in the model (Tab. 2).

Above the identified deflation breakpoints for significant variables, the number of species per plot kept on increasing, but more slowly. The rate of increase in rare species richness slightly slows down after the value of 1 fungus-bearing tree per ha in beech forests, and after the value of 29 deadwood types in the surrounding 0.3 ha in oak forests. The accumulation rate of common species slows down after a 17% openness in oak stands and a 2% openness in beech stands. In oak forests, the number of common species increased more slowly after the values of 11 deadwood types in the surrounding 0.3 ha, 1 fungus-bearing tree per ha, 46 m^3 of downed deadwood per ha.

In both beech and oak plots, the effect of deadwood diversity on species richness was partitioned into its four basic dimensions (diameter, tree species, decay, position [i.e. downed, standing or stump]). We did not measure any sharp contrasts between AICc values of linear mixed models including all combinations of the 4 deadwood dimensions for common and rare species (Fig. 1). The full model was never the most parsimonious model. The best model included (i) the number of combinations between positions and tree species, and to a lesser extent simply the diversity of deadwood positions (ΔAICc=1) for rare and common species in beech forests, (ii) the diversity of tree species, and to a lesser extent of diameter classes ΔAICc=2) for rare species and (iii) the number of combinations crossing tree species, diameter and decay stages for common beetle species in oak forests. Although the most structuring deadwood dimensions for species richness were not strictly consistent between oak and beech, and between common and rare species, the number of tree species was generally outstanding (Fig. 1).

Both deadwood diversity indices, the simple number and the Shannon diversity index of deadwood types, were similarly correlated to the deadwood volume (Spearman rho=0.48 for the simple index, rho=0.49 for the Shannon index). In both beech and oak data, the explanatory power of the Shannon model was only slightly better than the simple model (ΔAICc=4).

Response of individual species to openness

30% and 36% of tested species (102 species in beech stands, 189 species in oak stands) had a significant response to openness in beech and oak data, respectively (Tab. 5). In both beech and oak data, 77% of the significant species responses related to open-preferring species, and only 23% to shade-preferring taxa (whose abundance decreased with increasing stand openness). Among open-preferring species, 30% species were known to have flower-visiting adults. Contrarily, we did not find any known flower-visiting species among shade-preferring taxa. Only a few species displayed contrasting responses to openness in oak and beech data (Tab. 5).

Discussion

1. Local ecological drivers of saproxylic beetle diversity in temperate deciduous forests

Stand openness, a key feature

To summarize, among the diverse features describing local forest conditions for saproxylic beetles, both deadwood diversity and stand openness were consistent key habitat features for species richness and composition in oak and beech forests. The more open the deciduous forest, the higher the number of common species per plot in beech and oak forests, and the number of rare species in oak stands. Variations in species composition were mainly determined by the openness and the deadwood diversity in the oak plots, by site and large tree predictors in the beech plots. Moreover, a high proportion of the tested species displayed a significant response to openness (30% and 36% in beech and oak data, respectively). Our study confirms that canopy closure is clearly an outstanding attribute of the surrounding environment for saproxylic (even rare) beetles (Stokland et al., 2012). We here observed the same high proportion (77%) of open-preferring species among significant species responses in oak and beech forests. This strong influence of openness on both species richness and composition could relate (i) to an ecological complementation effect, between neighboring deadwood for larvae and flowers for adults, (ii) to microclimatic effects on sun-exposed substrates (and therefore habitat suitability of deadwood, fungi and other microhabitats on trees), as demonstrated in temperate forests by Vodka et al., (2009), and (iii) to thermodynamic effects on beetle activity, with more flying-active species in open and sun-exposed environments. Concerning the first point, we respectively detected 30% and 0% flower-visiting species among open- and shade-preferring taxa. Our analyses also indicated that the accumulation rate of common species slows down after a 17% openness in oak stands and a 2% openness in beech stands. Contrary to what we had expected, we did not observe humpback curves with two breakpoints, i.e. a decrease in richness after a second breakpoint due to the disappearance of species in extreme sun-, wind- and light-exposed substrates. The potential influence of a trappability bias (window-flight traps may be more efficient in open areas) has not been elucidated (Widerberg et al., 2012).

Density and diversity of deadwood

Overall, deadwood diversity was actually a more consistent predictor of species richness than deadwood ratio and downed or standing deadwood volumes. Its co-linearity with the total deadwood volume (Spearman correlation=0.49) prevents from disentangling their relative effects. The deadwood diversity significantly affected the species richness in beech and oak forests (as well as the species composition in oak forests). In other words, the higher the local number of deadwood types, the higher the number of common species per plot, and the number of rare species in oak stands. Our overall results confirm that the diversity of deadwood substrates plays an outstanding role in saproxylic diversity, as several previous studies have shown (e.g. Brin et al., 2009, Økland et al., 1996, Stokland et al., 2004). A wider range of resources (i.e. more various types of resource

present in exploitable amounts) hosts more specialists and as many generalist species. Among the 4 dimensions describing deadwood diversity (position, decay, diameter, tree species), the local number of (deciduous) tree species was a key element for species richness.

The deadwood ratio (the proportion of deadwood in total local wood volume, alive and dead), accounting for the wide natural variability in deadwood amounts over space and time due to the productivity of the forest and stand dynamics (Siitonen, 2001), did not better fit the relationship between deadwood amount and species richness than absolute deadwood volume.

Some studies have pointed out that the decline in deadwood quantity due to commercial forestry is stronger for some deadwood types, mainly snags and large logs (Sippola et al., 1998). These two components are therefore particularly at risk in managed forests. It has already been shown that oak and beech snags (Bouget et al., 2012; Brunet and Isacsson, 2009) and large logs (Brin et al., 2011; Økland et al., 1996) are key deadwood types for saproxylic beetles. In our study, the volumes of downed and standing deadwood did not provide significant intrinsic contributions to assemblage composition in oak and beech plots. The best models of species richness in lowland forests never included the standing deadwood. However, it should be noted that, in a companion study (Bouget et al., in prep.), the density of large standing deadwood was the second predictor of species richness in highland beech forests. Deadwood drivers clearly depend on the forest context.

In oak stands, the number of common species also significantly increased with the volume of all downed deadwood (the second best predictor after openness), and to a lesser extent, with the volume of large downed deadwood, both being even more influent than the deadwood diversity. Large deadwood volume did not affect the number of rare species, even though certain rare species are known to be sensitive to large log volume (Siitonen and Saaristo, 2000). Possibly the threshold we set for large deadwood (>40 cm), given for boreal forests by Nilsson et al. (2002), was too low to reflect ecological processes or should be modified for temperate contexts. Possibly species depending on large logs might be simply missing in managed forests due to the scarcity of large deadwood pieces.

Tree microhabitats as key resources?

In addition to canopy closure and deadwood resources; microhabitat features, as newly studied features, had weak but significant effects.The number of common species in oak stands and rare species in beech forests significantly increased with the density of fungus-bearing trees. Moreover the density of cavity-bearing trees had a slight positive impact on the common species richness in oak stands. However, in beech and oak forests, the density of cavity-, fungus-, deadwood-

, sap-run-bearing trees did not explain variations in species composition. The role of tree microhabitats for saproxylic assemblages remains insufficiently understood (Winter and Möller, 2008). Several saproxylic beetle species are known to be associated to cavities and tree holes (Ranius, 2002), to sap runs (Yoshimoto et al., 2005), to crown deadwood (Bouget et al., 2011) and lignicolous fungi (Jonsell and Nordlander, 2002).Microhabitats borne by live trees can occur in forests with a low total amount of deadwood. In our data, the density and diversity of microhabitats on trees and deadwood were not correlated.

Grove (2002b), Nilsson et al. (2002) and Ranius (2002) all suggested that the density of large trees could be important for certain saproxylic beetle species, since the presence of such trees reflects both habitat continuity and microhabitat supply. In our dataset, the density of large trees actually only correlated to the density of deadwood-bearing trees, but not to the density of cavity-, of fungus- and of sap-run-bearing trees. In our results, the density or basal area of large or very large trees did not explain local species richness either at a 0.3 ha scale or at a 1-ha scale. Nevertheless, variations in species composition were co-determined by site and large tree predictors in the beech plots.

The weak relationships observed between microhabitats and beetle fauna may be attributed to deficiencies (i) in beetle sampling and/or (ii)in the microhabitat surveys , and (iii) to the strong co-linearity among microhabitat variables in the modeled data. In beech data multiple joint effects between close variables or between environmental and spatial variables, made it difficult to decipher influences. In interpreting the results, we consequently should bear in mind that the present samples enable to reveal only strong effects. First,our beetle dataset is based on two window-flight traps per plot, set up during 1 year only. However, it has been demonstrated that the number of species detected at the plot level could be deeply increased by year or trap replication (Parmain et al., in press). Since the sampled assemblage may be poorly representative of the local fauna, it may weaken the analysis of the species-environment relationships. Moreover, it should be underlined that freely hanging window-flight traps are meant to catch active flying beetle species, and that (mostly rare) microhabitat-specialists, e.g. cavity-specialists, are only occasionally caught in these traps, unless a large sample size is set up. To study these groups, special kinds of targeted surveys or trapping methods are needed (Ranius and Jansson 2002). Our conclusions regarding rare species should be considered cautiously, since it is well known that (i) representative local catches of rare species require repeated sampling efforts (Martikainen and Kaila, 2004), and (ii) rare species dependent on higher amounts of deadwood are difficult to model due to their low abundance in trap catches. Secondly, except for crown deadwood, the microhabitats were only measured on trunks and on live trees. The real density of cavities was probably underestimated, especially for oak with frequently-

occurring cavities on large low branches within the tree crown. The density of lignicolous fungi, used as a proxy for fungal resources, was also undoubtedly underestimated since only large fruiting bodies were surveyed and one fungus at most was recorded per tree in the protocol. Moreover, the leaf cover may have hindered observations of microhabitats on the trunk; this could also have contributed to an underestimation of their number. The relationships between saproxylic and microhabitat diversity therefore require further investigations though such tree microhabitat surveys may be costly.

2. Perspectives

Perspectives for bio-indicator validation

Deadwood has become a centerpiece for forest monitoring in Europe. Since assessing stand structural elements is much faster and easier than inventorying species, deadwood is being widely used to indicate the conservation value of forests (Noss, 1999). More precisely, deadwood volume is considered to be an important indicator of forest biodiversity (Larsson, 2001) and, as such, has been selected by the European Environmental Agency as an assessment criterion for sustainable forest management practices (EEA, 2007). However, a validation of deadwood indicators at a wide geographical scale is still lacking (Stokland et al., 2004). Large downed deadwood volume was a significant predictor of beetle species richness in oak forests only. Deadwood diversity provided more consistent predictive models of the local number of saproxylic beetle species than volume variables in deciduous forests. In coniferous forests, deadwood diversity has also proven to be a better predictor of species richness than volume (pine: Brin et al, 2009, fir and spruce: Bouget, pers. com.). Using diversity variables can reduce the time spent sampling deadwood since presence/absence data from each type category is sufficient (Brin et al., 2009). Other studies have demonstrated that deadwood diversity is an efficient surrogate for many forest-dwelling species presence, including taxa that are not directly dependent on deadwood (e.g. Fritz et al., 2008). Finally, when we combined deadwood diversity and microhabitat diversity (i.e. the number of both deadwood and microhabitat types) in a single additive index, there was only a negligible increase in explanatory power on beetle species richness, compared with deadwood diversity alone (from R^2=0.33 to R^2=0.34 in all deciduous plots). The validation of ecologically-relevant indirect biodiversity indicators which are easy to survey based on data from national forest inventories, would require further large-scale and multi-taxonomic analyses. These features will also serve as criteria for more effective selection of conservation areas.

Implications for forestry

Substantial evidence exists that commercial forestry has a negative impact on deadwood quantity (Fridman and Waldheim, 2000). Several studies have reported that the diversity of deadwood substrates is also altered by forestry (e.g. Ekbom et al. 2006). We found that deadwood diversity is a consistent key factor for saproxylic beetle diversity; we therefore suggest that forest managers favor the local diversification of deadwood types rather than any given target volume (but see below in oak forests). From our analyses, deadwood positions and tree species were key dimensions for the effect of deadwood diversity on species richness; overall, the number of tree species was outstanding. In managed forests, forestry is known to induce (i) a depleted local diversity of tree species in deadwood, due to the counter-selection of many native tree species that are not considered economically valuable, and (ii) a decreased local diversity of deadwood positions, mainly due to the elimination of standing deadwood, perceived as a safety hazard (Bishop et al., 2009). It therefore seems relevant to increase the number of combinations of positions and tree species (except introduced exotic species) to favour the local species richness of saproxylic beetles. Moreover, further ecological studies should pay more attention to mixed coniferous-deciduous forests.

Our statistical breakpoints of deadwood or microhabitat values in the accumulation rate of species can not be translated into management targets as ecologically meaningful aggregation of true species extinction thresholds. It should however be borne in mind that threshold analyses did not consider the spatial structure of the data, despite the importance of site effects. Nonetheless, they may inspire cost-effective management guidelines. For instance, the efforts to retain just 1 fungus-bearing tree per ha would significantly increase beetle species richness and would be cost-effective. In our data, the strongest increase in rare species richness in beech forests and in common species in oak forests indeed occurred from 0 to 1 fungus-bearing tree per ha. The rate of increase in species richness actually slightly slows down beyond the value of 1 tree per ha.In oak forests, an effort of downed deadwood restoration up to the target of 50m3 per ha would be efficient from an ecological perspective (though a bit costly in terms of forestry benefits), since the number of common species increased more slowly with deadwood volume beyond the value of 46 m3 per ha. Nevertheless, it should be made clear that such quantitative deadwood targets would not meet the needs of all species; deadwood-dependent species are extremely numerous, and their deadwood requirements are species-specific (Müller and Butler, 2010). Finally, since stand openness strongly affected species composition, deadwood and microhabitats should be managed both under closed-canopy and open conditions (Vodka et al., 2009).

Perspectives for further approaches

One shortcoming of most of the empirical studies on saproxylic organisms is that they are typically conducted at a single, relatively small spatial scale. However, the probability of occurrence of saproxylic beetles is known to increase with the amount of dispersal sources in the surrounding landscape (e.g. Gibb et al., 2006). Moreover, habitat distribution may be more important than habitat quality in fragmented forest areas (Brunet and Isacsson, 2009) like the temperate forests in Western Europe. One explanation for the lack of clear results on the relationship between deadwood or microhabitat density and biodiversity may be that resources have not been measured over an area large enough to reflect deterministic influences on local beetle assemblages, especially for aerially dispersing beetle species (Bishop et al., 2009). To date, only a few studies have shown the positive effects of deadwood volume on local saproxylic beetle species richness (Franc et al., 2007; Gibb et al., 2006; Økland et al., 1996) or deadwood-rich stands (Franc et al., 2007) in the surrounding landscape (from 100 m to 1 km). Considering the effects of regional deadwood on local assemblages might make a better spatial match between inventories and ecological processes (Turner and Tjørve, 2005). Even if stand specific deadwood thresholds supply some information about the local richness and abundance of a species group, landscape-level deadwood thresholds would be necessary when considering the viability of meta-populations (Ranius and Fahrig, 2006).

Local assemblages may also be considerably affected by delayed effects of past gaps in the continuity of the local deadwood supply, continuity which is critical for species long-term persistence (Jonsell and Nordlander, 2002). Including more data about the history of deadwood availability would improve the explanatory power of assembly rules in saproxylic communities.

Acknowledgements

We are grateful to Y. Paillet, A. Lassauce, C. Moliard (Irstea), T. Noblecourt, T. Barnouin, F. Soldati (ONF), N. Debaive (RNF), J. Willm, L. Burnel (INRA) and all the local forest managers for their field and laboratory work, and to F. Gosselin for helpful comments during the project, and Vicki Moore who checked the English language, and two anonymous reviewers whose detailed comments deeply improved our manuscript. This research was funded by the French Ministry in Charge of the Ecology through the BGF program (convention RESINE CVOJ000150, convention 10-MBGD-BGF-1-CVS-092, n°CHORUS 2100214651) and the National Forestry Board (ONF-Cemagref convention, Action 5,

2008). Part of this work was funded by the French Environment and Energy Management Agency (ADEME).

References

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. Ecology 84: 511-525.

Bishop DJ, Majka CG, Bondrup-Nielsen S, Peck SB (2009) Deadwood and saproxylic beetle diversity in naturally disturbed and managed spruce forests in Nova Scotia. Zookeys 22: 309-340.

Bouget C, Brustel H, Zagatti P, Noblecourt T, 2010. The French information system on saproxylic beetle ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation statuts. http://frisbee.nogent.cemagref.fr/index.php/en/ Accessed 15 January 2013

Bouget C, Brin A, Brustel H (2011) Exploring the last biotic frontier: are temperate forest canopies special for saproxylic beetles? Forest Ecol Manag 261: 211-220.

Bouget C, Nusillard B, Pineau X, Ricou C (2012) Effect of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags. Insect Conserv Diver 5: 264-278.

Brin A, Bouget C, Brustel H, Jactel H (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. J Insect Conserv 15: 653-669.

Brin A, Brustel H, Jactel H (2009) Species variables or environmental variables as indicators of forest biodiversity: a case study using saproxylic beetles in maritime pine plantations. Ann For Sci 66: 1-11.

Brunet J, Isacsson G (2009) Influence of snag characteristics on saproxylic beetle assemblages in a south Swedish beech forest. J Insect Conserv 13: 515-528.

Burnham KP Anderson DR (eds) (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Berlin.

Cobb TP; Hannam KD; Kishchuk BE, Langor DW, Quideau SA, Spence JR (2009) Wood-feeding beetles and soil nutrient cycling in burned forests: implications of post-fire salvage logging. Agr Forest Entomol 12(1): 9-18.

Dodelin B, André J, Wlérick L, Lempérière G (2004) Le bois mort en forêt de montagne (Alpes françaises). R. F. F. 66: 507-518.

EEA (2007) Halting the loss of biodiversity by 2010: proposal for a first set of indicators to monitor progress in Europe. Luxembourg: European Environment Agency, 186 p. ISBN 978-92-9167-931-7

Ekbom B, Schroeder LM, Larsson S (2006) Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. Forest Ecol Manag 221: 2-12.

Franc N, Gotmark F, Okland B, Norden B, Paltto H (2007) Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. Biol Conserv 135: 86-98.

Frank AF (2011) R-hacks / mer-utils.R. https://github.com/aufrank/R-hacks/blob/master/mer-utils.R. Accessed 15 January 2013

Fridman J, Walheim, M (2000) Amount, structure and dynamics of deadwood on managed forestland in Sweden. Forest Ecol Manag 131: 23-36.

Fritz O, Gustafsson L, Larsson K (2008) Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biol Conserv 141: 655-668.

Gibb H, Hjältén J, Ball JP, Atlegrim O, Pettersson RB, Hilszczanski J, Johansson T, Danell K (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. Ecography 29: 1-14.

Grove SJ (2002a) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst. 33: 1-23.

Grove SJ (2002b) Tree basal area and deadwood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecol Indic 1: 171-188.

Hothorn T, Hornik K, Zeilis A (2006) Party: a laboratory for recursive part(y)itioning (2006) http://CRAN.R-project.org/ Accessed 20 August 2012

Jonsell M, Nordlander G (2002) Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of deadwood. Forest Ecol Manag 157: 101-118.

Larjavaara M, Muller-Landau HC (2010) Comparison of decay classification, knife test and two penetrometers for estimating wood density of coarse woody debris. Can J Forest Res 40: 2313-2321.

Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Can J Forest Res 42: 1433-1445.

Larsson TB (Ed) (2001) Biodiversity evaluation tools for European forests. Ecol Bull 50: 1-240.

Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol Indic 11: 1027-1039.

Martikainen P, Kaila L (2004) Sampling saproxylic beetles: lessons from a 10 year monitoring study. Biol Conserv 120: 171-181.

Martikainen P, Siitonen J, Punttila P, Kaila L, Rauh J (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol Conserv 94: 199-209.

Müller J, Bütler R (2010) A review of habitat thresholds for deadwood: a baseline for management recommendations in European forests. Eur J For Res 129: 981-992.

Nilsson SG, Niklasson M, Hedin J, Aronsson G, Gutowski JM, Linder P, Ljungberg H, Mikusinski G, Ranius T (2002). Densities of large living and dead trees in old-growth temperate and boreal forests. Forest Ecol Manag 161: 189-204.

Noss RF (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. Forest Ecol Manag 115: 135-146.

Økland B, Bakke A, Hagvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiv Conserv 5: 75-100.

Päivinen J, Ahlroth P, Kaitala V, Suhonen J (2003) Species richness and regional distribution of myrmecophilous beetles. Oecologia 134: 587-595.

Parmain G, Dufrene M, Brin A, Bouget C (in press) Influence of sampling effort on saproxylic beetle diversity assessment. Implications for biomonitoring studies in European temperate forests. Agr Forest Entomol 15: 135-145

Ranius T (2002) Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol Conserv 103: 85-91.

Ranius T, Fahrig L (2006) Targets for maintenance of deadwood for biodiversity conservation based on extinction thresholds. Scan J Forest Res 21: 201-208.

Ranius T, Jansson N (2002) A comparison of three methods to survey saproxylic beetles in hollow oaks. Biodiv Conserv 11: 1759-1771.

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms : Fennoscandian boreal forests as an example. Ecol Bull 49: 11-41.

Siitonen J, Martikainen P, Punttilä P, Rauh J (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecol Manag 128: 211-225.

Sippola A, Siitonen J, Kallio R, (1998) Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish lapland. Scan J Forest Res 13: 204-214.

Stokland JN, Tomter SM, Söderberg GU (2004) Development of deadwood indicators for biodiversity monitoring: Experiences from Scandinavia, in: Marchetti M (ed) Monitoring and indicators of forest biodiversity in Europe—From Ideas to Operationality. European Forest Institute, EFI proceedings n°51, pp. 207-226.

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in deadwood. Cambridge University Press.

Turner WR, Tjørve E (2005) Scale-dependence in species-area relationships. Ecography 28: 721-730.

Vodka S, Konvicka M, Cizek L, (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. J Insect Conserv 13: 553-562.

Koch Widerberg M, Ranius T, Drobyshev I, Nilsson U, Lindbladh M (2012) Increased openness around retained oaks increases species richness of saproxylic beetles Biodiv Conserv 21: 3035-3059

Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecol Manag 255: 1251-1261.

Yoshimoto J, Kakutani T, Nishida T (2005) Influence of resource abundance on the structure of the insect community attracted to fermented tree sap. Ecol Res 20: 405-414.

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1: 3-14.

Table. 1 Description of structural (deadwood, microhabitats, large trees, openness, forest type) variables and study sitesexplored in the study.

		BEECH		OAK	
		Mean +/- SE	range	Mean +/- SE	range
Deadwood	Total volume of deadwood in a 0.3ha plot (m^3/ha)	66.561+/-11.771	0-371	28.131+/-2.676	0-123
	Volume ratio=deadwood /(Live trees+deadwood)	0.213+/-0.031	0-1	0.107+/-0.009	0-0.5
	Nb deadwood types (tree species*diameter*decay*position)	10.122+/-0.816	1-28	19.971+/-1.254	1-53
	Volume of standing deadwood (>10 cm in diameter) in a 0.3ha plot (m^3/ha)	18.284+/-4.357	0-128	4.886+/-0.922	0-65
	Volume of large standing deadwood (> 40 cm in diameter)) in a 0.3ha plot (m^3/ha)	14.705+/-4.336	0-128	2.801+/-0.818	0-65
	Volume of downed deadwood (>10 cm in diameter) in a 0.3ha plot (m^3/ha)	48.277+/-8.953	0-287	20.657+/-2.379	0-111
	Volume of large downed deadwood (>40 cm in diameter) in a 0.3ha plot (m^3/ha)	21.537+/-5.698	0-209	4.2+/-1.186	0-101
Microhabitat	Total density of microhabitat-bearing trees in a 1ha plot	16.918+/-1.744	0-52	17.663+/-1.031	3-50
	Number of microhabitat types in a 1ha plot	4.469+/-0.260	0-7	4.779+/-0.135	1-7
	Density of cavity-bearing trees in a 1ha plot: "empty" cavities with an entrance above 3 cm in width, woodpecker breeding and feeding holes, deep cavities formed between roots, cavities with mould with an entrance above 10 cm in width	7.612+/-0.713	0-18	5.558+/-0.396	0-20
	Density of fungus-bearing trees in a 1ha plot: fruiting bodies of tough or pulpy saproxylic fungi, >5cm in diameter,	1.306+/-0.238	0-7	0.942+/-0.115	0-7
	Density of deadwood-bearing trees a 1ha plot: crown deadwood in (large dead branches > 20 cm in diameter and > 1 m in length, crown deadwood volume > 20% of the total crown wood volume)	6.02+/-1.052	0-37	8.096+/-0.742	0-31
	Density of sap-run-bearing trees: sap runs > 10 cm in length in a 1ha plot	0.286+/-0.071	0-2	0.423+/-0.083	0-4

Large trees	Number of very large trees in a 1ha plot (dbh>67. 5cm)	4.816+/-1.035	0-32	12.25+/-1.181	0-51
	Basal area of very large trees in a 0.3ha plot (67.5<dbh ≤87.5 cm) (m^2/ha)	1.768+/-0.481	0-15	5.611+/-0.602	0-30
	Basal area of the largest trees in a 0.3ha plot (dbh>87.5 cm) (m^2/ha)	0.982+/-0.361	0-14	0.753+/-0.208	0-12
Openness	Open areas (clearings, edges, areas with a well developed herb layer composed of flowering plants) (%) in a 1ha plot	10.792+/-2.883	0-100	15.228+/-2.734	0-100
Forests	Beech or oak	49 plots, 98 traps		104 plots, 208 traps	
	Auberive (AUB)	15 plots, 30 traps		9 plots, 18 traps	
	Chize (CHZ)	12 plots, 24 traps		12 plots, 24 traps	
	Citeaux (CIT)			12 plots, 24 traps	
	Combe-Lavaux (CL)	5 plots, 10 traps		3 plots, 6 traps	
	Fontainebleau (FBL)	17 plots, 34 traps		7 plots, 14 traps	
	Rambouillet (RBT)			30 plots, 60 traps	
	Troncais (TR)			31 plots, 62 traps	

Table. 2. Variance inflation factor (VIF) of predictor variables selected in the linear mixed reduced models of species richness (with forest as a random effect), to be used in the model averaging approach (after sequential selection; Zuur et al., 2010), for addressing the multicollinearity problem. The VIF represents the proportion of variance in one predictor explained by all the other predictors in the model. A VIF = 1 indicates no collinearity. All selected VIFs were below a pre-defined cutoff of 3 (as suggested by Zuur et al., 2010)

Predictor (covariate)	Oak	Beech
Deadwood diversity	2.26	2.24
Deadwood ratio		2.33
Volume of standing deadwood (logx+1)	2.79	2.41
Volume of large standing deadwood (logx+1)	2.70	
Volume of downed deadwood (logx+1)	2.26	
Volume of large downed deadwood (logx+1)	1.77	
Density of very large trees	1.71	
Basal area of largest trees	1.99	1.70
Density of cavity-bearing trees	2.34	2.34
Density of fungus-bearing trees	1.82	1.74
Density of deadwood-bearing trees	1.46	1.61
Density of sap-run-bearing trees	1.47	1.64
Microhabitat diversity	2.33	
Openness	1.41	1.53

Table. 3. Canonical Analysis of Principal coordinates (CAP) used to partition the variation in the response species-plot matrix with respect to the combination of explanatory stand features (deadwood, microhabitat, large trees, openness); %NSCI: relative contribution to the non-spatial constrained inertia. Only significant variables (** 0.01>p>0.001, * 0.05>p>0.01, ° 0.1>p>0.05) were selected.

		Oak plots			Beech plots		
	Variable	Total inertia	Marginal Inertia	%NSCI	Total inertia	Marginal Inertia	%NSCI
Deadwood	Volume of deadwood (logx+1)	0.481 **	ns	3.5 %	0.589 *	ns	
	Deadwood ratio		ns		0.529 **		
	Deadwood diversity		0.406 *		0.465 *		
	Volume of standing deadwood (logx+1)				0.591 **		
	Volume of large standing deadwood (logx+1)				0.548 *		
	Volume of downed deadwood (logx+1)				0.582 *		
	Volume of large downed deadwood (logx+1)				0.664 *		
Microhabitat	Microhabitat density	0.404 *	ns		ns	ns	
	Microhabitat diversity	0.485 *			0.453 °		
Large trees	Basal area of very large trees	0.420 *	ns		0.723 **	ns	
	Density of very large trees	ns			0.592 **		
	Basal area of largest trees				0.761 **		
Openness	openness	0.663	0.445 *	3.9 %	0.513	ns	

		**			**		
Spatial	forest	11.415 **	5.120 **		3.392 **	2.181 **	

Table. 4. Multi-model averaged estimates for structural stand features (deadwood, microhabitats, large trees, openness) determining the response of saproxylic beetle species richness (rare, common). Relative importance is the weight of evidence for each parameter across all the best models combining several variables (mixed-effect models, with forest as a random effect). Only significant variables (*** p<0.001, ** 0.01>p>0.001, * 0.05>p>0.01, ° 0.1>p>0.05) were selected. Significant relationships in SR response were searched for breakpoints (significance p<0.001, 80% Confidence Interval based on 5000 bootstrap samples).

Forest type	species richness	Predictor	Model-averaged estimate (significance)	Relative contribution	Deflation breakpoint	Best models (Delta AICc<3)	
Oak	Rare	Deadwood diversity	1.66 **	0.81	29 [19-30]	Deadwood diversity + openness	AICc=421.1
		openness	0.81 *	0.34	No		
	Common	openness	9.0 ***	0.99	17 [3-80]	Volume of downed deadwood + openness	AICc=767.9
		Volume of downed deadwood (logx+1)	9.4 ***	0.94	46 [12-47]		
		Volume of large downed deadwood (logx+1)	7.7 ***	0.04	No		
		Deadwood diversity	10.0 **	0.01	11 [10-17]		
		Density of fungus-bearing trees	5.4 **	0.01	1 [1-3]		
		Density of cavity-bearing trees	4.3 °	0.01	No		
Beech	Rare	Density of fungus-bearing trees	1.09 *	0.56	1 [1-3]	Density of fungus-bearing trees	AICc=181.5
	Common	openness	14.38 ***	0.97	2 [1-10]	Deadwood diversity + openness	AICc=378.0
		Deadwood diversity	6.27 °	0.24	No		

Table 5. Response in abundance of selected beetle species to stand openness.

Only species caught in more than 10 individuals and occurring in more than 10% samples were analyzed using a Generalized Linear Mixed Model with a Poisson error distribution, and "forest" as a spatial random effect. Only significant responses were displayed (*** p<0.001, ** 0.01>p>0.001, * 0.05>p>0.01). Species with well-known flower-visiting adults (Bouget et al. 2010) were underlined.

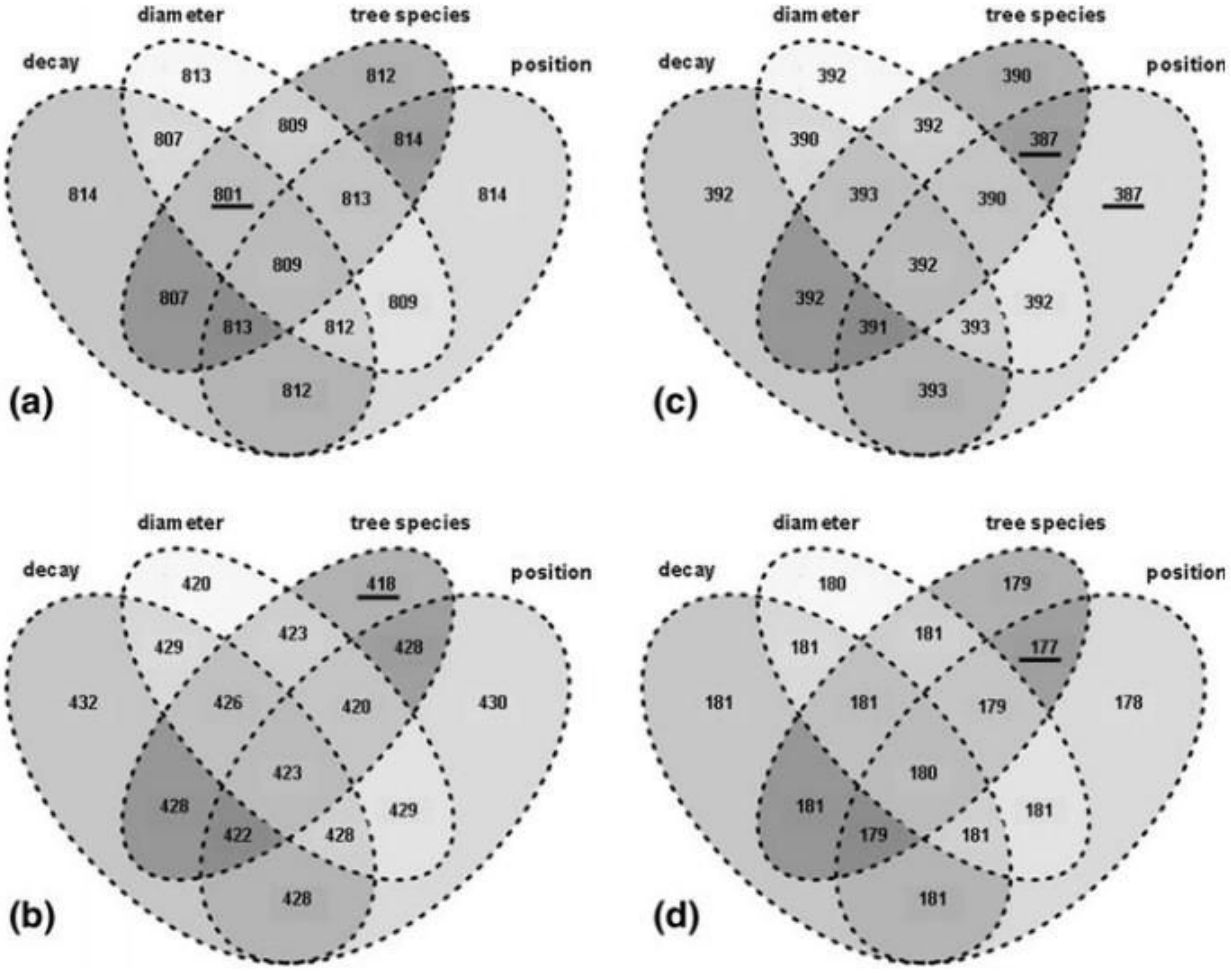
Shade-preferring species		Open-preferring species	
Oak stands	beech stands	oak stands	beech stands
Anobium.hederae ***, Hemicoelus.fulvicornis ***, Isoriphis.melasoides ***, Leiopus.femoratus ***, Melasis.buprestoides *, Mycetophagus.piceus *, Ochina.ptinoides *, Orchesia.undulata *, Pediacus.dermestoides ***, Tetratoma.ancora ***, Vincenzellus.ruficollis ***, Xyleborinus.saxesenii ***	Aulonothroscus.brevicollis *, Diplocoelus.fagi *, Platystomos.albinus *	Abdera.bifasciata **, Agrilus.sp ***, Alosterna.tabacicolor *, Ampedus.cinnaberinus *, Ampedus.sanguinolentus **, Anaspis.fasciata *, Anaspis.frontalis ***, Anaspis.melanopa ***, Cis.boleti **, Clerus.mutillarius ***, Clytus.arietis *, Colydium.elongatum ***, Cortinicara.gibbosa ***, Cortodera.humeralis ***, Cryptarcha.undata ***, Cryptolestes.duplicatus **, Dasytes.aeratus **, Dasytes.plumbeus ***, Dryocoetes.villosus ***, Epuraea.sp ***, Gonodera.luperus ***, Megatoma.undata **, Mycetochara.maura ***, Mycetophagus.atomarius *, Pachytodes.cerambyciformis *, Paromalus.parallelepipedus *, Pediacus.depressus *, Placonotus.testaceus ***, Plegaderus.dissectus **, Prionus.coriarius **, Ptinus.bidens ***, Ptinus.subpilosus *, Rhagium.sycophanta **, Rhizophagus.bipustulatus *, Rhizophagus.depressus ***, Silvanus.unidentatus *, Stenurella.melanura ***, Thanasimus.formicarius ***, Triplax.lepida *, Tritoma.bipustulata	Ampedus.glycerus ***, Corticarina.similata *, Cyclorhipidion.bodoanus ***, Enicmus.brevicornis ***, Glischrochilus.quadriguttatus *, Laemophloeus.monilis ***, Leptura.aurulenta **, Melanotus.villosus *, Microrhagus.lepidus ***, Nemozoma.elongatum ***, Platycerus.caraboides **, Stenocorus.meridianus ***, Tomoxia.bucephala ***

		***, Tropideres.albirostris ***, Xyleborus.dryographus ***	
Hemicoelus.costatus **, Trypodendron.domesticum **, Xyleborus.dispar ***, Xylosandrus.germanus ***		Cerambyx.scopolii ***, Cetonia.aurata ***, Cryptarcha.strigata ***, Dacne.bipustulata ***, Litargus.connexus ***, Pyrochroa.coccinea **, Scolytus.intricatus ***, Taphrorychus.bicolor ***, Triplax.russica ***, Valgus.hemipterus **, Xyleborus.monographus ***	
Species with contrasting response in oak and beech data			
Microrhagus.pygmaeus * Isoriphis.marmottani *** Salpingus.planirostris *** Ernoporicus.fagi ***	Hylecoetus.dermestoides **	Hylecoetus.dermestoides ***	Microrhagus.pygmaeus *** Ernoporicus.fagi *** Isoriphis.marmottani *** Salpingus.planirostris **

Figure captions

Figure. 1. Partitioning of the deadwood diversity effect on common and rare species richness into its four basic dimensions (diameter class, decay class, tree species, position) and all their combinations in beech and oak plots. All mixed models (with forest as a random factor) for all combinations of the 4 deadwood properties were compared using AICc values. The four-set Venn diagram with simple ellipses displays all 24-1=15 possible areas created by the interaction of 4 sets. The Venn diagram was not scaled, i.e. the graphical size of each intersecting or non-intersecting area is not proportional to the numerical AICc value. The best model is underlined.

a) and (b): oak forests, c) and d): beech forests ; a) and c): common species, b) and d): rare species



Synthèse de l'article 6

Article	Problématiques	Résultats Habitat	Résultats coléoptères saproxyliques	Points discutés	Questions soulevées	Perspectives d'étude	Conclusions
6	Nous souhaitons mieux connaitre les relations existant entre environnement et biodiversité associées et déterminer : (i) les éléments structurels clés indicateurs de la richesse en espèce des coléoptères saproxyliques, (ii) améliorer les consignes de gestion forestière pour une gestion durable. Nous avons principalement tenté de (i) démêler les liens entre éléments du milieu (conditions abiotiques, densité et diversité des ressources) qui sont supposés structurer les communautés de coléoptères saproxyliques en forêt de feuillus et (ii) déterminer si les éléments clés du milieu sont constants entre chênaies et hêtraies.	Non testé.	Déterminants des assemblages d'espèces: *Chêne:* diversité du bois mort (3.5%); quantité et densité en dendromicrohabitat; surface de gros arbres; Ouverture du milieu; Spatial (forêt). *Hêtre*: Log volume bois mort; ration bois mort/bois total; diversité du bois mort; volume bois mort debout; volume gros bois mort debout; volume bois mort au sol; volume gros bois mort au sol; diversité en dendromicrohabitats; surface de gros arbres; densité de gros arbres; surface du plus gros arbre; ouverture du peuplement; Spatial (forêt). Richesse spécifique: *Chêne*: *Espèces communes*: Ouverture du milieu; log volume bois mort au sol; log volume gros bois mort au sol; diversité de bois mort; densité d'arbres porteurs de fructifications de champignons lignicoles; densité d'arbres porteurs de cavités. *Espèces rares*: Diversité du bois mort; Ouverture du milieu. *Hêtre: Espèces communes*: Ouverture du milieu; diversité du bois mort. Espèces rares: densité d'arbres porteurs de fructifications de champignons lignicoles. Effets du bois mort sur la richesse spécifique: *Chêne: Espèces communes*: essence*diamètre*degré de décomposition sont les plus efficaces pour expliquer les variations de richesse spé. *Espèces rares*: essence seule est la plus efficace pour expliquer les variations de richesse spé. *Hêtre: Espèces communes*: essence*position sont les plus efficaces pour expliquer les variations de richesse spécifique. *Espèces rares:* essence*position ont les plus efficaces pour expliquer les variations de richesse spécifique. Effets de l'ouverture sur les espèces: *Chêne:* plus d'espèces préfèrent les conditions ouvertes (77%).Parmi ces espèces, 30% ont des adultes floricoles. Pas d'espèces avec adultes floricoles parmi les espèces préférant les conditions ombragées. *Hêtre*: mêmes observations.	Effet de l'ouverture du milieu sur les espèces saproxyliques. Diversité de bois mort comme point clé de la richesse en espèces saproxyliques. Certains éléments du bois mort sont particulièrement retirés des forêts exploitées (gros bois au sol et debout).	L'augmentation d'espèces contactées dans des zones plus ouvertes est elle due à une réalité écologique ou à un biais méthodologique du polytrap? Espèces dépendantes des stades avancés de la sylvigenèse absentes des forêts gérées par cause de disparition de leur habitat? Quel est la contribution des dendromicrohabitats à la conservation n des insectes saproxyliques par rapport au bois mort?	Evaluation de la pertinence du volume de bois mort comme indicateur de la richesse spécifique par l'étude de plusieurs groupes taxinomiques su une grande échelle. Va permettre une meilleure sélection des zones à conserver. Besoin de mener des études à large échelle. Besoin de prendre en compte la structure passée de l'environnement étudié.	Le volume et diversité de bois mort sont des éléments clés structurant les assemblages et la richesse des coléoptères saproxyliques. Cependant, ces patterns varient en fonction du type forestier étudié (forêts de chêne ou hêtre dans notre cas). Les dendromicrohabitats ont également un rôle particulier, mais la nouveauté de l'étude de ces structures n'a pas encore permis de mettre en place des protocoles permettant de les considérer efficacement.

Tableau 4 : In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Problématiques, résultats, éléments particuliers discutés, nouvelles problématiques posée, perspectives d'études à envisager et conclusions principales de l'article.

Article 3: Extended rotations in French oak forests do not enhance saproxylic beetle diversity.

Parmain, G. et Bouget, C. (et al)

Article en préparation.

Résumé :

La qualité d'habitat est un facteur essentiel pour la survie des espèces. Dans un contexte forestier fortement impacté par l'activité humaine, la préservation de la biodiversité est assurée en soustrayant des zones forestières à l'exploitation. Le rôle des structures permanentes pour la préservation de la biodiversité est actuellement relativement mal appréhendé. Mais ces zones représentent un manque à gagner élevé pour le gestionnaire forestier. Afin de concilier des objectifs de production et de conservation de la biodiversité, des structures de protection temporaires ont été proposées. Il s'agit de retarder ponctuellement l'exploitation de la parcelle durant 25 ou 50 ans pour maintenir un habitat favorable aux espèces saproxyliques.

Nous avons évalué le rôle joué par ces structures sur la préservation de la biodiversité forestière à travers le prisme des coléoptères saproxyliques. Nous avons étudié la réponse des coléoptères saproxyliques à la mise en place d'ilots de vieillissement en futaie de chêne du nord de la France. Nous n'avons observé aucune modification significative des compartiments favorables aux coléoptères saproxyliques entre placettes témoin et post-traitement. Le nombre d'espèces de coléoptères saproxyliques contacté entre les deux types de placettes n'était pas significativement différent, et ce même pour les espèces rares. Parmi les variables environnementales étudiées, seule l'ouverture du milieu avait une influence sur l'abondance des espèces contactées.

Nous avons mis en évidence la neutralité de l'extension de rotation de peuplements maturs avec maintien des activités sylvicoles vis-à-vis des caractéristiques structurelles du milieu. Aucun impact positif ou négatif sur les cortèges de coléoptères saproxyliques n'a été détecté. La stratégie de rallongement du cycle sylvicole pour les phases matures des peuplements n'apparait pas comme une stratégie pertinente pour la conservation des coléoptères saproxyliques.

Introduction

La biodiversité forestière est largement impactée par l'exploitation forestière (Martikainen *et al.,* 2000 ; Similä *et al.,* 2003 ; Penttilä *et al.,* 2004). Par son action, les habitats caractéristiques associés aux stades terminaux du cycle sylvigétnétiques disparaissent (Gilg, 2004). Ces éléments sont des habitats privilégiés pour une vaste communauté d'organismes, les organismes saproxyliques (dépendant du bois mort).

Différentes mesures de conservation de cette biodiversité saproxylique sont actuellement disponibles. La plupart du temps, cela consiste à soustraire de l'activité humaine des portions d'habitat, afin que celui-ci retrouve progressivement un caractère naturel. Ces zones peuvent être définies a priori, sur la base d'une capacité d'accueil présumée de la biodiversité. Pourtant, elles sont plus efficaces si elles sont sélectionnées sur la base de la biodiversité qu'elles abritent (Timonen *et al.,* 2010). Les plus efficaces sont sans doute les réserves forestières de grande taille, car elles permettent de produire une grande quantité et diversité d'habitats favorables au cours du temps (Lachat et Bütler, 2007). Elles sont cependant contraignantes à mettre en place. Des structures de conservation plus petites leur sont généralement préférées (Tscharntke *et al.,* 2002). Ces structures peuvent être mises en place lors de l'exploitation finale des peuplements. Des groupes d'arbres sont retenus dans le peuplement exploité. Ces éléments sont retrouvés en Europe mais également en Amérique. On les appelle des *Green Tree Retention patches* (GTR, Gustafsson *et al.,* 2010). Leur efficacité pour la préservation d'une partie de la biodiversité forestière est reconnue (Rosenvald et Lohmus, 2008). Cependant, cet effet n'est mesuré que sur de courtes périodes post-exploitation. Dans les pays Scandinaves, des petits patches d'habitat sont également préservés. Ils sont appelés des Woodland Key Habitats (WKH, Timonen *et al.,* 2010). Ils sont sélectionnés à priori, sur la base de caractéristiques d'habitat favorables à la biodiversité, en particulier de la biodiversité saproxylique. Pourtant, leur efficacité de conservation est rarement éprouvée (Timonen *et al.,* 2010).

Ces différentes structures sont généralement laissées en libre évolution une fois mises en place, et aucune récolte de bois n'y est effectuée. Elles vont accumuler des structures particulières favorables à la conservation de la biodiversité saproxylique. Ces éléments peuvent être répartis en trois classes sommaires : le bois mort, les dendromicrohabitats et les arbres vivants de forts diamètre (Krauss et Krumm, 2013 ; Gilg, 2004 ; Stockland *et al.,* 2012).

Les arbres de fort diamètre sont un élément central occupant le gestionnaire et le naturaliste. En effet, les gros arbres en forêt sont synonymes de richesse en espèces (Grove, 2002b). Ces arbres ont également une importance économique majeure (Jaret, 2004 ; Sardin, 2008). Ils sont particulièrement rares en forêts exploitées (Lindenmayer *et al.,* 2012). Dans l'optique de concilier préservation de la biodiversité et production de bois de grande valeur économique, une structure de conservation propre aux forêts françaises a été proposée, les ilots de vieillissement. Ils sont constitués par des peuplements où le cycle sylvicole va être rallongé. La coupe définitive sur ces peuplements sera retardée d'une durée variable, entre 25 et 50 ans (ONF, 2009).

Durant la durée d'allongement du cycle, les interventions sylvicoles sont permises afin de récolter tout arbre présentant des signes de dépréciation économique, ou menaçant un autre arbre de qualité. Ces ilots sont généralement mis en place sur des surfaces de l'ordre de l'hectare, parfois moins. Cette mesure de conservation est récente (ONF, 2009) et son efficacité est encore mal évaluée (Lassauce *et al.,* 2013).

Partant de ce constat, nous nous posons les questions suivantes :

- Quel est l'impact des extensions des cycles sylvicoles avec maintien de l'activité finale d'exploitation sur les compartiments écologiques « bois mort » et « dendromicrohabitats » ?
- Quel est l'impact de ces modifications de milieu sur les assemblages de coléoptères saproxyliques ?

Matériel et méthodes

Sites d'étude

Notre objectif était de comparer les peuplements forestiers de futaie de chêne bénéficiant des effets de la mesure conservatoire que sont les ilots de vieillissement. Le gradient créé par l'extension d'une seule durée d'aménagement (entre 25 et 30 ans) nous a semblé trop faible pour détecter de quelconques différences de structure ou de composition en espèces. Bouget *et al,* (2014) ont en effet montré que la réponse des coléoptères saproxyliques à l'augmentation de qualité d'habitat était très faible après 30 ans de non-exploitation stricte.

L'exploitabilité des arbres est déterminée par leur diamètre ; celui-ci est généralement de 70cm en chênaie du nord de la France (Jaret, 2004 ; Sardin, 2008). L'application de la mesure de conservation ilots de vieillissement permet un accroissement théorique du diamètre des arbres variable entre 6 et 12cm (accroissement annuel d'environ 2.5mm). Les peuplements issus d'ilots de vieillissement devraient alors avoir des proportions d'arbres de diamètre de 80cm et plus supérieures aux peuplements matures. Nous avons choisi de nous placer dans le cas où le peuplement aurait subi deux extensions de rotations (produisant des arbres de 80cm de diamètre). Nous avons considéré que les placettes avec une proportion d'arbres de diamètre 70 et 80 cm supérieure à 70% étaient des peuplements matures, en fin de cycle sylvicole, prêts à être exploités. Nous les avons définis comme les placettes témoin. Les placettes avec une proportion d'arbres de diamètre plus grand que 80cm supérieure à 30% étaient des peuplements en fin de phase étendue d'exploitation. Ils correspondaient alors à la définition d'ilots de vieillissement arrivés à terme. Nous avons défini ces placettes comme post-traitement.

Nous avons étudié 11 chênaies du nord de la France. Dans chacune des forêts, en fonction des disponibilités de peuplements à très gros arbres présents, nous avons défini un nombre variable de placettes témoin et post traitement (Tableau 1). Au total, ce sont 81 pièges à interception qui ont été mis en place.

Matériel d'étude

Les Coléoptères saproxyliques ont été échantillonnés à l'aide de pièges à interception de type polytrap. Les pièges étaient distants d'au moins 50m entre eux. Les pièges ont été suspendus grossièrement à 1.50 m du sol. La faune circulante a été échantillonnée en 2012, d'Avril à Août. Le mélange conservateur et non attractif des pièges était constitué par un mélange de 50% de Mono Propylène Glycol (MPG) de qualité alimentaire, de sel et d'un agent tensio-actif (détergent neutre, sans parfum).

Les familles suivantes présentant des difficultés d'identification élevées ont été écartées des données (Clambidae, Cantharidae, Malachiidae, Dryopidae, Ptiliidae, Scirtidae, Scydmaenidae, Staphylinidae incl. Scaphidiinae & Pselaphinae). Pour chaque espèce au sein des familles identifiées, nous avons caractérisé son degré de rareté a priori en se référant à la base en ligne FRISBEE (http://frisbee.nogent.cemagref.fr/ index.php/en/). Nous avons défini pour chaque placette les variables insectes : la richesse totale en espèces saproxylique (RStot), l'abondance totale des espèces

saproxyliques (ABtot), la richesse spécifique des espèces saproxyliques rares (RSrar) et l'abondance des espèces saproxyliques rares (ABrar).

Variables environnementales

Les mesures environnementales ont été conduites en hiver. L'ouverture du milieu a été définie comme l'ouverture de la canopée dans un rayon de 20m autour du centre de placette. Cette estimation a été menée par le même opérateur sur la totalité des placettes.

L'estimation du volume de bois mort à l'hectare a été faite en adaptant le protocole proposé par (Lassauce *et al.,* 2013). Trois transects de 20m de long ont été installés à 0, 133 et 267 grad en partant du centre de la placette. Le bois mort au sol de faible diamètre (entre 2.5 et 32.5cm de diamètre) intersecté par le transect a été mesuré (diamètre). Le volume de bois mort de plus de 32.5cm de diamètre (debout ou au sol) a été estimé par cubage des pièces concernées dans un rayon de 20m autour du centre de la placette. Les parties du tronc de moins de 30cm de diamètre ou qui sont en dehors du cercle de 20m n'ont pas été prises en compte. Le volume bois de mort sur pied (7.5 à 32.5 cm) a été estimé dans un rayon de 10m autour du centre de la placette. Pour chacune des pièces de bois mort considérées, nous avons renseigné l'essence ainsi que le niveau de dégradation, estimé à l'aide du 'test du couteau' (Mäkinen *et al.,* 2006) et de la surface d'écorce présente. Nous avons identifié trois stades de dégradation du bois, correspondant à trois degrés de pénétration de la lame dans le bois (1 : dur, la lame ne s'enfonce quasiment pas ; 2 : pénétration partielle de la lame ; 3 : pénétration totale de la lame). Trois niveaux de présence d'écorce ont été définis (1 : présente sur toute la pièce ; 2 : partiellement présente ; 3 : totalement absente de la pièce). L'indicateur de diversité du bois mort a été obtenu en créant des « espèces de bois mort » qui seront composées de la classe de diamètre de la pièce de bois, de son essence, et de son niveau de dégradation (bois + écorce).

Le nombre d'arbres avec un DBH (Diameter at Breast Height) entre 70 et 80cm, et un DBH supérieur à 80cm a été compté dans des cercles d'un rayon de 20 et 56m autour du piège. Pour chacun de ces arbres, le nombre et la nature de dendromicrohabitats présents ont été comptés. Nous avons défini 6 types différents de dendromicrohabitats : *Cavité* (regroupe les cavités en eau, à terreau, trous de pics avec diamètre minimal d'entrée de 5cm), *Ecorce* (regroupe décollement d'écorce, fente), *Bois apparent* (regroupe plage de bois sans écorce, plage de bois cariée), *Champignons* (champignon saproxylique coriace), *Lierre* (présence de lierre sur au moins 20% du tronc), *Houppier* (regroupe bois mort dans le houppier et charpentière brisée).

La richesse et la diversité en dendromicrohabitats, le nombre de *Cavité* et le nombre moyen de dendromicrohabitats par arbre ont été mesurés pour les arbres avec un DBH supérieur à 70cm dans un rayon de 20 ou 56 m autour de chaque piège. Les différentes variables utilisées sont synthétisées dans le Tableau 2.

Analyses

Nos objectifs principaux étaient d'étudier (i) les changements de structure des peuplements suite au rallongement du cycle sylvicole (ii) l'impact que ces changements ont sur les assemblages de coléoptères saproxyliques (RStot, Abtot, Rsrar, Abrar et composition).

Les différences de caractéristiques structurelles retenues entre les deux types de placettes (pré-rallongement et post-rallongement) ont été comparées avec un test de Kruskal-Wallis.

La normalité des variables Rstot, Abtot, RSrar, ABrar a été testée avec la méthode de Shapiro-Wilks.

Nous avons utilisé des modèles linéaires généralisés et mixtes pour évaluer l'effet des caractéristiques du milieu sur les coléoptères saproxyliques. Les variables suivant une loi de distribution de type gaussienne seront analysées avec un modèle LMER (fonction lmer dans le package R lme4) et les variables suivant une loi de distribution poisson avec un modèle GLMER (fonction glmer dans le package R lme4). Nous avons utilisé un facteur appelé « Obs » pour limiter la sur-dispersion des données dans les modèles utilisant les variables insectes suivant une loi de poisson. La forêt a été utilisée comme facteur aléatoire dans les modèles.

Les variables environnementales structurantes pour les assemblages de coléoptères saproxyliques (toutes espèces ou espèces rares uniquement) ont été recherchées par une procédure d'analyse canonique en composantes principales (vegan R-package, CAP, Anderson et Willis, 2003).

Résultats

Nous avons collecté 28296 coléoptères et identifié 550 espèces. Parmi elles, 395 ont été définies en tant que saproxyliques et représentent 14042 individus. Parmi ces espèces, 47 (11.89%) sont considérées comme rares.

Caractéristiques structurelles

Le rallongement du cycle sylvicole n'a pas provoqué de changement significatif de l'ouverture du milieu, ni d'augmentation du volume de bois mort total ni de la diversité du bois mort. Dans les placettes où le cycle sylvicole a été rallongé, on observe un plus grand nombre de dendromicrohabitats (à 0.3 et 1ha). La diversité en dendromicrohabitats est également plus grande dans les placettes où le cycle sylvicole a été rallongé (à 0.3 et 1ha). En revanche, il n'y a pas de différence significative du nombre moyen de dendro-microhabitats portés par les arbres avec un diamètre supérieur à 70 cm à 20 ou 56 m du centre de la placette (Tableau 3).

Facteurs influençant la richesse et l'abondance des espèces

Nous n'avons pas observé de différence significative en nombre d'espèces totales ou rares pas plus que de différences d'abondance entre les placettes témoin et les placettes post extension.

Au sein des placettes témoin, seule l'abondance totale des espèces était positivement influencée par l'ouverture du milieu. Toutes les autres variables ne présentaient pas d'effet significatif sur la richesse totale ou rare, ni sur l'abondance totale ou des espèces rares.

Au sein des placettes post-traitement, l'abondance de la totalité des espèces était significativement positivement influencée par la diversité en dendromicrohabitats à l'hectare portés par les arbres au DBH supérieur à 70 cm ainsi que par l'ouverture du milieu. Toutes les autres variables ne présentaient pas d'effet significatif sur la richesse totale ou des espèces rares, ni sur l'abondance totale ou des espèces rares (Tableau 4).

Facteurs influençant la composition en espèces

Aucun paramètre testé n'influence significativement les assemblages d'espèces totales ou rares, ni dans les placettes témoin, ni dans les placettes post-traitement.

Discussion

Caractéristiques structurelles

L'allongement de rotation n'a pas eu d'influence sur le volume ni la diversité totale de bois mort au niveau de la placette. En revanche, la quantité et la diversité des dendromicrohabitats est supérieure sur les placettes de 0.3 et 1ha post-traitement. Cependant, le nombre moyen de dendromicrohabitats par arbre de plus de 70cm de diamètre n'est pas significativement différent entre les deux types de traitements. Ceci suggère que la quantité de dendromicrohabitats n'augmente pas avec l'extension de la rotation du peuplement. Nous avons montré (Bouget *et al.,* 2014) qu'un minimum de 30ans de mise en réserve (non-exploitation) était nécessaire à une reconstitution partielle des stocks de bois mort et de dendromicrohabitats. Un ilot de vieillissement est mis en place sur une durée variable entre 25 et 50 ans (ONF, 2009), avec le maintien de l'activité sylvicole, et laisse peu de chances aux structures favorables aux coléoptères saproxyliques de se régénérer. Lassauce *et al,* (2013) ont trouvé des résultats similaires sur la non-modification des caractéristiques structurelles du milieu entre des placettes de 180/200 ans et 200/220 ans. En revanche, des changements significatifs étaient observés entre les placettes 180/220 ans et les +300ans. Lassauce *et al,* (2012) ont montré que l'extension de rotation du cycle du taillis (de 20 à 60 ans) avait un affect significatif sur les caractéristiques structurelles du milieu. A la différence de la futaie mature, le stade du taillis est caractérisé par la croissance rapide de nombreuses tiges de l'essence cible. Cette forte croissance et compétition entre les tiges provoque la mort de certaines d'entre elles. Ce phénomène propre au taillis pourrait expliquer les différences de résultats observés.

Influence sur les cortèges d'espèces saproxyliques

Les ilots post-traitement n'abritent pas plus d'espèces totales ou rares que les ilots témoin. L'abondance totale des espèces est influencée par l'ouverture du milieu, quel que soit le type de

placette considéré. L'abondance de la totalité des espèces est de plus influencée par la diversité en dendromicrohabitats à l'hectare au sein des placettes post-traitement. L'ouverture du milieu et la diversité en dendromicrohabitats sont des variables reconnues pour fortement impacter la richesse spécifique, l'abondance et la composition des communautés saproxyliques (Sverdrup-Thygesson et Ims, 2002 ; Horak et Rébl, 2013 ; Bouget *et al.,* 2013 ; Larrieu, 2014).

Les assemblages d'espèces ne sont influencés par aucune des variables étudiées. Les compartiments d'habitat ayant des effets positifs sur les assemblages (Bouget *et al.,* 2014 ; Bouget *et al.,* 2013) ne sont ici pas différents entre les deux types de traitement. De plus, leur quantité est faible comparativement aux volumes observés dans des zones non exploitées (Siitonen *et al.,* 2000).

Différence entre extension du cycle et mise en réserve temporaire ou définitive

D'un point de vue conceptuel, les ilots de vieillissement sont mis en place pour satisfaire deux objectifs contraires : la production de bois de qualité et la préservation de la biodiversité. Ils permettent ainsi de produire des bois de grande qualité (Sardin, 2008 ; Jaret, 2004) tout en maintenant des structures reconnues comme favorables à la biodiversité (des arbres de fort diamètre). Mais, au sein de ces structures, les opérations d'exploitation forestière sont autorisées, si certaines tiges viennent à présenter des défauts susceptibles d'impacter la valeur économique de l'arbre, ou des arbres voisins (ONF, 2009). Cette structure de conservation temporaire est différente des '*temporary set aside elements*' dans lesquels toute intervention est proscrite, et le milieu est laissé en libre évolution pendant la durée d'exclusion de l'exploitation. Ceci permet la reconstitution d'une partie des éléments favorables à la biodiversité saproxylique (Bouget *et al.,* 2014) qui ne peuvent être obtenus si l'exploitation est également maintenue.

Surface critique des mesures conservatoires forestières

Nous avions pour objectif d'apporter des éléments pratiques à la mise en place des ilots de vieux bois. Nous avons entrepris de comparer l'effet des variables environnementales susceptibles d'être impactées par l'extension de rotation sur les coléoptères saproxyliques à deux échelles spatiales restreintes, 0.3 et 1ha. Nous n'avons observé qu'un seul effet significatif de la diversité en microhabitats sur l'abondance totale des espèces, celui-ci étant effectif à l'échelle de l'hectare. La surface minimale de 1ha pour les mesures de conservation de type ilots forestiers est mise en avant (*Green Tree Retention* (GTR) (Gustafsson *et al.,* 2010) ou Woodland Key Habitats (WKH, Timonen *et al,* 2010)). Cependant, des surfaces de conservation plus grandes de l'ordre de la centaine d'hectares sont requises pour obtenir une diversité et quantité importantes de bois mort continues au cours du temps (Lachat et Bütler, 2007), que des surfaces plus faibles auront du mal à générer.

Piège écologique

Un piège écologique se définit comme un habitat de faible qualité sélectionné par une espèce au lieu d'un habitat de meilleure qualité (Battin, 2004). Dans le cadre des forêts, un habitat

de bonne qualité pour les espèces saproxyliques va être défini comme une zone suffisante pour générer une quantité et diversité de bois mort et dendromicrohabitats de manière continue dans le temps pour permettre le maintien des populations locales. Cette définition rassemble toutes les zones non exploitées de manière définitive telles les réserves et les ilots de sénescence. Par opposition, les habitats de mauvaise qualité seront les zones forestières restantes, les zones exploitées. Nous avons montré qu'il n'y avait pas de différence en nombre d'espèces ni d'abondance totale entre les placettes témoin et les placettes post-traitement. Ceci indique que les zones post traitement ne sont pas de meilleure qualité que les zones témoin. Les zones post traitement (les ilots de vieillissement arrivés à terme) ne constituent de ce fait pas un plus grand piège écologique que les zones témoin.

Conclusions et perspectives

Nous avons mis en évidence la neutralité de l'extension de rotation de peuplements matures avec maintien des activités sylvicoles vis-à-vis des caractéristiques structurelles du milieu. Aucun impact positif ou négatif sur les cortèges de coléoptères saproxyliques n'a été détecté. La stratégie de rallongement du cycle sylvicole pour les phases matures des peuplements forestiers n'apparait pas comme une stratégie pertinente pour la conservation des coléoptères saproxyliques de chênaie de plaine du nord de la France.

L'importance que peut avoir l'extension courte de rotation (40ans) en milieu forestier a cependant été mise en évidence par Lassauce *et al,* (2012) dans un système de taillis. L'efficacité de l'extension du cycle sylvicole pourrait être différente entre les traitements sylvicoles et des durées. La compréhension de ces phénomènes en fonction des contextes nécessite des recherches sur d'autres contextes (taillis sous futaie, peuplement méditerranéens, forêts de montagne…).

Bibliographie

Anderson, M.J. Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* **84**, 511–524.

Battin, J. (2004) When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology,* **18**: 1482-1491.

Bobiec, A. (2002) Living and dead wood in the Bialowieza forest: suggestions for restoration management. *Forest ecology and Management* **165**: 125-140.

Bouget, C. Larrieu, L. Nusillard, B. Parmain, G. (2013) In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation* **22**: 2111–2130.

Bouget, C. Parmain, G. Gilg, O. Noblecourt, T. Nusillard, B. Paillet, Y. Pernot, C. Larrieu, L. Gosselin, F. (2014) Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? *Animal Conservation* **17**: 342–353.

Gilg, O. (2004) *Forets à caractère naturel. Caractéristiques, conservation et suivi*. Réserves Naturelles de France, Gestion des milieux et des Espèces, Cahiers techniques n°74. 96p.

Grove, S.J. (2002) Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. *Ecological Indicators* **1**: 171–188.

Gustafsson, L. Kouki, J. Sverdrup-Thygeson, A. (2010) Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences, Scandinavian *Journal of Forest Research* **25**:4, 295-308,

Horak, J. Rébl, K. (2013). The species richness of click beetles in ancient pasture woodland benefits from a high level of sun exposure. *Journal of Insect Conservation* **17**:307–318.

Jaret, P. (2004) *Guide des sylvicultures. Chênaie atlantique*. ONF, Paris, 335p.

Kraus, D. Krumm, F. (eds) (2013) *Integrative approaches as an opportunity for the conservation of forest biodiversity*. European Forest Institute. 284 pp.

Lachat, T. Bütler, R. (2007). *Gestion des vieux arbres et du bois mort. Ilots de sénescence, arbres-habitat et métapopulations saproxyliques*. Mandat de l'Office fédéral de l'environnement. Lausanne: 87.

Larrieu, L. (2014) *Les dendro-microhbitats: facteurs clés de leur occurrence dans les peuplements forestiers, impact de la gestion et relations avec la biodiversité taxonomique*. Université de Toulouse, 115p.

Lassauce, A. Anselle, P. Lieuthier, F. Bouget, C. (2012) Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: A case study in French deciduous forests. *Forest Ecology and Management* **266**: 273–285.

Lassauce, A. Larrieu, L. Paillet, Y. Lieuthier, F. Bouget, C. (2013) The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation lengths in a French oak high forest. *Insect Conservation and Diversity* **6**: 396–410.

Lindenmayer, D.B. Blanchard, W. McBurney, L. Blair, D. Banks, S. Likens, G.E. Franklin, J.F. Laurance, W.F. Stein, J.A.R. Gibbons, P. (2012) Interacting Factors Driving a Major Loss of Large Trees with Cavities in a Forest Ecosystem. *PLoS ONE* **7**: e41864. doi:10.1371/ journal.pone.0041864

Mäkinen, H. Hynynen, J. Siitonen, J. Sievänen, R. (2006) Predicting the decomposition of Scots pine, Norway spruce and birch stems in Finland. *Ecological Applications* **16**: 1865–1879.

Martikainen, P. Siitonen, J. Punttila, P. Kaila, L. Rauh, J. (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation* **94**: 199-209.

ONF, (2009) Conservation de la biodiversité dans la gestion courante des forêts publiques. INS-09-T-**71**: 11.

Penttilä, R. Siitonen, J. Kuusinen, M. (2004) Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. *Biological Conservation* **117**: 271–283.

Rosenvald, R. Lohmus, A. (2008) For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management* **255**: 1–15.

Sardin, T. (2008) *Guide des sylvicultures. Chênaies continentales*. ONF, Paris. 455p.

Siitonen, J. Martikainen, P. Punttila, P. Rauh, J. (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management* **128**, 211–225.

Similä, M. Kouki, J. Martikainen, P. (2003) Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management* **174**: 365–381.

Stokland, J. Siitonen, J. Jonsson, B.G. (2012). *Biodiversity in dead wood.* Cambridge university press, 509p.

Sverdrup-Thygeson, A. Ims, R.A. (2002) The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biological Conservation* **106**: 347–357.

Timonen, J. Siitonen, J. Gustaffson, L. Kotiaho, J. Stockland, J.N. Sverdrup-Thygesson, A. Mökkönen, M. (2010) Woodland key habitats in northern Europe: concepts, inventory and protection. *Scandinavian Journal of Forest Research* **25**: 309-324.

Tscharntke, T. Steffan-Dewenter, I. Krues, A. Thies, C. (2002) Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research* **17**: 229–239.

Tables

Situation géographique	Forêt (dept)	Nombre total de pièges	Témoin	Post-traitement
Centre	Saint Palais	9	6	3
E	Lisle	12	3	9
E	Mont-Dieu	6	4	2
E	Signy l'Abbaye	9	3	6
E	Traconne	6	3	3
E	Bezange	9	1	8
W	Bercé	6	3	3
W	Candé	6	3	3
W	Loches	6	2	4
W	Montgoger	6	4	2
W	Réno-Valdieu	6	3	3
Total général		81	35	46

Tableau 1 : Répartition des pièges au sein des 11 forêts d'étude. « Situation géographique » : Appartenance au quart Nord-Est de la France (E); Nord-Ouest (W) ou au Centre. « Forêt (dept) » : Nom de la forêt d'étude avec département indiqué entre parenthèses. Témoin : placettes avec une proportion d'arbres au DBH compris entre 70 et 79 > 70% ; Post-traitement : placettes avec une proportion d'arbres au DBH supérieur à 80cm > 30%.

Openness	Surface cumulée de trouées dans la canopée estimée dans un rayon de 20m autour du piège. Valeur exprimée en pourcentage d'ouverture du milieu
BMT	Volume total de bois mort (m^3/ha)
divbm	Diversité du bois mort (espèce*diamètre*décomposition du bois*degré décollement écorce)
nbmh20	Nombre total de dendromicrohabitats portés par les arbres de DGH>70cm dans un rayon de 20m autour du piège
nbmh56	Nombre total de dendromicrohabitats portés par les arbres de DGH>70cm dans un rayon de 56m autour du piège
divmh20	Nombre total de types différents de dendromicrohabitats portés par les arbres de DGH>70cm dans un rayon de 20m autour du piège
divmh56	Nombre total de types différents de dendromicrohabitats portés par les arbres de DGH>70cm dans un rayon de 56m autour du piège
meannbMH.tree.70_20m	Nombre moyen de dendromicrohabitats portés par les arbres de DBH>70cm dans un rayon de 20m autour du piège
meannbMH.tree.70_56m	Nombre moyen de dendromicrohabitats portés par les arbres de DBH>70cm dans un rayon de 56m autour du piège
meandivmh20	Nombre moyen de types différents de dendromicrohabitats portés par les arbres de DBH>70cm dans un rayon de 20m autour du piège
meandivmh56	Nombre moyen de types différents de dendromicrohabitats portés par les arbres de DBH>70cm dans un rayon de 56m autour du piège

Tableau 2 : Variables environnementales utilisées.

	Cat1 (< 30% DBH>79)	Cat2 (> 30% DBH>79)	Sign
Openness	0.2 (0.11568212)	0.1913043 (0.08452767)	ns
BMT	21.45005 (15.34211)	22.37995 (13.92938)	ns
divbm	8.114286 (2.730777)	8.173913 (2.293027)	ns
nbmh20	2.514286 (1.930733)	**3.891304 (3.253909)**	*
nbmh56	10.02857 (6.723469)	**14.30435 (6.383554)**	**
divmh20	1.428571 (0.9166985)	**1.934783 (0.9522412)**	*
divmh56	2.514286 (1.541035)	**3.434783 (1.128464)**	**
meannbMH.tree.70_20m	0.9488095 (0.9027512)	1.0792443 (0.7608256)	ns
meannbMH.tree.70_56m	0.8094683 (0.4261202)	0.925526 (0.3644479)	ns
meandivmh20	0.6378571 (0.721182)	0.6121032 (0.3835863)	ns
meandivmh56	0.2369212 (0.1665653)	0.2320187 (0.09612614)	ns

Tableau 3 : Résultats des différences structurelles observées entre les placettes avant extension de rotation, et les placettes post extension. Test de Kruskal-Wallis.

	Placettes témoin				Placettes post-traitement			
	Toutes espèces		Espèces rares		Toutes espèces		Espèces rares	
	Richesse spécifique	Abondance	Richesse spécifique	Abondance	Richesse spécifique	Abondance	Richesse spécifique	Abondance
BMT	ns	ns	ns	ns	ns	ns	ns	ns
divbm	ns	ns	ns	ns	ns	ns	ns	ns
nbmh20	ns	ns	ns	ns	ns	ns	ns	ns
nbmh56	ns	ns	ns	ns	ns	ns	ns	ns
divmh20	ns	ns	ns	ns	ns	ns	ns	ns
divmh56	ns	ns	ns	ns	ns	*	ns	ns
Openness	ns	**	ns	ns	ns	**	ns	ns
meannbMH.tree.70_20m	ns	ns	ns	ns	ns	ns	ns	ns
meannbMH.tree.70_56m	ns	ns	ns	ns	ns	ns	ns	ns
meandivmh20	ns	ns	ns	ns	ns	ns	ns	ns
meandivmh56	ns	ns	ns	ns	ns	ns	ns	ns

Tableau 4 : Résultats des lmer et glmer.

Synthèse de l'article 3

Article	Problématiques	Résultats Habitat	Résultats coléoptères saproxyliques	Points discutés	Questions soulevées	Perspectives d'étude	Conclusions
3	Quel est l'impact des extensions des cycles sylvicoles avec maintien de l'activité finale d'exploitation sur les compartiments écologiques bois mort et dendromicrohabitats ? Quel est l'impact de ces modifications de milieu sur les assemblages de coléoptères saproxyliques ?	Aucun effet	**Placettes témoin***: Richesse spécifique: Toutes espèces*: pas de réponse. *Espèces rares*: pas de réponse. *Abondance: Toutes espèces*: Ouverture du milieu. *Espèces rares*: pas de réponse. **Placettes post-traitement:** *Richesse spécifique: Toutes espèces*: pas de réponse. *Espèces rares*: pas de réponse. *Abondance: Toutes espèces*: Ouverture du milieu; diversité en dendromicrohabitats à l'hectare. *Espèces rares:* pas de réponse. **Assemblages**: pas de réponses de la part des variables étudiées	Durée de non exploitation pour observer des modifications d'habitat. Durée d'extension de rotation.	Les zones exploitées à retardement sont-elles des pièges écologiques? Peuvent-elles servir de source pour les peuplements voisins?	Etudier de plus longues périodes d'extension de rotation. Étudier l'impact des ilots de vieillissement (ou peuplements matures) sur les populations de zones voisines.	Pas d'effet positif ou négatif des ilots de vieillissement pour la diversité des coléoptères saproxyliques.

Tableau 5 : Extended rotations in french oak forests do not enhance saproxylic beetle diversity. Problématiques, résultats, éléments particuliers discutés, nouvelles problématiques posée, perspectives d'études à envisager et conclusions principales de l'article.

Partie II : Les éléments non forestiers

Les constituants de la TTVB en milieu non forestiers sont diversifiés. Il peut s'agir d'une bande d'arbres riverains à un cours d'eau, un bosquet, un parc de ville, un alignement, un arbre isolé dans un jardin ou un champ…. L'évaluation de leur participation à la conservation des coléoptères saproxyliques est un sujet récent. La quantité de ces éléments implique la mise en place d'un dispositif d'échantillonnage constitué de nombreux pièges si la contribution de chacun de ces éléments doit être évaluée au regard des autres.

Nous avons choisi de nous intéresser à une structure particulière, les arbres isolés. Ces arbres sont des structures ponctuelles dans le paysage et constituent des points de concentration de la biodiversité (Manning *et al.,* 2006). La probabilité qu'un évènement catastrophique impacte l'arbre est accrue par son isolement (la probabilité d'être impacté diminue avec l'augmentation du nombre de cibles possibles). Leur intérêt pour la conservation est de ce fait disproportionné par rapport à d'autres éléments constitués de plus d'arbres (Fischer *et al.,* 2010).

Nous avons choisi d'étudier la contribution relative des chênes isolés à la conservation des coléoptères saproxyliques dans une matrice agricole dans deux paysages ateliers, l'Allier et l'Yonne. Cinq sites forestiers et non forestiers ont été échantillonnés de manière appariée. Les caractéristiques structurelles de l'arbre porteur du piège ainsi que diverses variables environnementales ont été comparées entre milieu forestier et milieu non-forestier. Les facteurs régissant les assemblages d'espèces en et hors forêt ont été explorés.

Les premiers résultats indiquent que le nombre d'espèces entre forêt et arbres isolés n'est pas significativement différent, mais que seulement 50% des espèces sont communes entre les deux milieux. La recherche d'espèces indicatrices de chacun des contextes (forestier et arbres isolé) a révélé que chaque milieu possède des espèces caractéristiques. Enfin, les déterminants de la richesse en espèces et de la composition des assemblages de coléoptères saproxyliques diffèrent en forêt et en milieu non forestier.

Nos résultats permettent de désigner les arbres isolés comme structures prioritaires de conservation à l'égard des coléoptères saproxyliques, en attendant que l'évaluation des autres éléments non-forestiers soit conduite. L'exploration de la contribution d'autres essences ligneuses que le chêne devra également être conduit.

Article 4: Are solitary trees keystone structures for saproxylic beetles associated with large oaks?

G. Parmain*/°/**, C. Bouget*

Article en préparation.

* National Research Institute of Science and Technology for Environment and Agriculture. (IRSTEA), 'Forest ecosystems' Research Unit, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France (christophe.bouget@irstea.fr; guilhem.parmain@irstea.fr).

° National Laboratory of Forest Entomology, National Forest Office (ONF), F-11500 Quillan, France. (guillem.parmain@onf.fr)

** National Museum of Natural History, Natural Patrimony Department, 36 rue Geoffroy St Hilaire, CP 41 75 231 PARIS CEDEX 05, France.

Abstract:

Nowadays, most of the saproxylic biodiversity conservation effort is focused on forests, and most responsibilities lies on forest managers. Solitary trees are of major interest for biodiversity conservation, in particular for saproxylic species. Few is known about their relative contribution to saproxylic diversity respect to forests. Using the particular group of saproxylic beetles, we studied five forest and solitary related trees sites in France in a paired design. We described the trap bearing tree structure and environmental characteristics. Our results highlighted major structural differences between forest and solitary tree contexts. We found as many microhabitats per Ha in forest as solitary context. Saproxylic beetles species richness nor abundance was not different between forest and solitary tree context. However, species assemblages were strongly dissimilar, with specialist species for each of our studied contexts. Also, main drivers of total and rare species richness or assemblages were closely related to trap bearing tree characteristics, in particular microhabitat number and diversity.

We discuss about the importance of solitary trees conservation and the possible example of oak solitary trees for forest habitat and retention trees at final harvesting.

Key-words: Saproxylic beetle, France, solitary tree, oak, habitat tree, retention tree.

Introduction:

1. Oak as a key tree species for saproxylic biodiversity

Saproxylic species depends on dead wood or tree microhabitats like cavities, bark loss or deadwood related fungi (Alexander, 2008). Numerous species are polyphagous on deciduous or conifer trees. Some are even polyphagous on both tree types like *Morimus asper* (Coleoptera, Cerambicydae). But there are also tree specialists. Some saproxylic beetle species are related to particular tree species like *Xylotrechus rusticus* for aspen in Fennoscandia (Sahlin and Schoreder, 2010), or *Osmoderma eremita*, mostly founded in oak cavities (Ranius and Nilsson, 1997). Among tree species, oak supports the richest and specialized (Jonsell *et al.,* 1998) saproxylic beetle community In Sweden (Palm, 1959), but also in Europe (Vodka *et al.,* 2009). Moreover, oak associated saproxylic beetles are one of the most endangered organisms groups in Europe (Jansson and Cozkun, 2008; Nieto and Alexander, 2010).

2. Habitat trees vs deadwood as keystone structures for saproxylic biodiversity

Deadwood volume and diversity are well known drivers of saproxylic beetles species richness and assemblages. But, according to Lassauce *et al,* (2011), the importance of dead wood strongly depends on forest context. Dead wood volume influence on saproxylic beetles was higher in boreal forests rather than temperate forests. Bouget *et al,* (2013) founded dead wood diversity to be more important for saproxylic beetles than dead wood volume in temperate forests. Microhabitats were more efficient drivers of species richness than dead wood volume was in temperate forests. According to Larrieu and Cabanettes (2012), tree microhabitat probability occurrence is not the same among tree species. This probability is higher on deciduous trees rather than coniferous trees. It also increases with tree diameter. Trees with microhabitat are called 'habitat trees' and are especially useful for saproxylic biodiversity conservation (Larrieu, 2014).

Oak sustain a large number of species across Europe. Besides, habitat trees are of primal interest for saproxylic beetle conservation. In managed temperate oak (or oak mixed) forests, habitat oak trees are logically of first interest for saproxylic beetles conservation.

3. Forest vs non-forest elements into saproxylic habitat networks

An old-growth forest possesses typical structural elements like large standing dead trees, and a high number and diversity of habitat trees (Gilg, 2004). Such elements disappeared in managed harvested forests, or are less frequent (Siitonen *et al.,* 2000). Together, they constituted a network of high quality habitat inside a harvested forest matrix. Saproxylic beetles species did not only rely on forest habitats. Urban parks (Jonssel, 2004; 2012), hedgerows (Dubois *et al.,* 2009), or solitary trees (Sverdrup-Thygesson *et al.,* 2010) are also supporting saproxylic rich species communities. Such elements are in general constituted by native large trees species (Manning *et al.,* 2006).

Forest harvesting impacted European forest for millennia (Grove, 2002a). Forest disappearance leads to total habitat surface reduction and increased distance between forest patches (Tscharntke *et al.,* 2002). In such fragmented landscape, non-forest elements are stepping stones and 'lifeboats' for saproxylic species (Matveinen-Huju *et al.,* 2006).

4. Relative contribution of forest vs non-forest oak trees to associated biodiversity

Forest and wooded non-forest elements are both parts of a landscape network of suitable habitats for saproxylic organisms. Long unmanaged or old-growth forests are known to be high conservation areas for saproxylic biodiversity. I contrast, the role of non-forest wooded elements in saproxylic biodiversity conservation is poorly known. Some studies enlighten the importance of such elements (Jonsell, 2004, 2012), but few ones compared them to related forests habitats (Sverdrup-Thygesson *et al.,* 2010).

Based on a paired design study between ok forests and solitary trees in 5 sites in French mainland, we address the following questions:

- Importance of forest vs non-forest oak trees for biodiversity conservation?
- Are solitary trees keystone structures for biodiversity conservation?
- Which tree attributes affect the ecological value of oak trees for spx biodiversity?

Material and methods:

Study area

We studied 5 French Oak forests, 3 in the Allier French department and 2 in the Yvelines French department. Each of them was called a 'site' in the following text. 88 traps were set up, 44 in forest and 44 on solitary trees; in a paired design (Tab. 1). In the Yvelines French department, forests were public forests. Solitary trees were in restricted areas used for presidential hunting. The particular management policy promotes wild game populations. It resulted in an open area matrix with very small patches of vegetation, with two or three large trees inside (trees with DBH>70cm).

In the Allier French department, forests were private forest. Solitary trees were found in private agro pastoral landscape, and are nowadays useless propriety separations.

Solitary trees can be strongly human impacted, due to pollarding (Sebek *et al.,* 2013) or cattle grazing damages. We compared forest trees with the closest aspect as possible as solitary trees. In forest, selected management type was coppice with standards.

Data collection (Beetle data)

Flying saproxylic beetles were sampled by using cross-vane flight interception traps (Polytrap^{TM}). In forest context, traps were grouped by pairs or triplets in forests stands. In each pair or triplet, traps were separated by at least 20m. Each group of traps was distant from 100m at least. In solitary tree context, we used only one trap per tree. Each trap in solitary tree condition was

separated by another one by 20m at least. As tree DBH influenced saproxylic beetles species richness (Ranius and Jansson, 2000), we chose trees with similar DBH between forest and solitary contexts.

Traps were hanged out at the first >35cm crown branch of large Oak trees. The active insect fauna was collected in 2013, from April to August. Conservative non-attractive liquid was made with 50% Mono Propylene Glycol (MPG), water, salt and tension-active agent (detergent).

The following saproxylic families, often difficult to identify at the species level (Clambidae, Dryopidae, Ptiliidae, Scirtidae, Staphylinidae incl. Scaphidiinae), were removed from the dataset. For each species in all the taxa from the remaining ±50 families recorded, we characterized the degree of geographic rarity in France according to the FRISBEE database (http://frisbee.nogent.cemagref.fr/index.php/en/).

We computed total species richness, total species abundance rare species richness and rare species abundance at the trap level. We focused on species richness because it seemed to be positively related to ecosystem functioning (Hector and Bagchi, 2007). A species-rich stand (in particular for rare species) will indicate a well working (i.e functioning) ecosystem or habitat.

Environmental variables

All field measurements were made in winter, to facilitate field work and access through ferns. Without leaves, more light passes through the branches and microhabitats in the top of trees were easier to observe.

As our lowest sampling unit was a trap on a large tree, all environmental variables were measured at the trap level, or around him. The trap bearing tree (**TbT**) was also described.

Dead wood measurements were made at a radius of 10m, 20m and 56 m around each trap. Small (between 2.5 to 32.5 cm in diameter) lying dead wood volume was estimated with three 20m-long transects at 0; 133 and 267 grad around the trap; Medium (between, 7.5 and 32.5cm diameter) standing dead wood volume was estimated in a radius circle of 10m around each trap. Large (more than 32.5cm diameter) lying and standing dead wood volume was assessed in a 20m radius circle around each trap. All volumes were converted at the Ha scale.

We characterized seven types of micro-habitats (or groups of microhabitats) favorable to saproxylic species: *cavities* (empty, woodpecker holes, dendrothelms…), *bark* (bark detachment, crack in the trunk), *visible wood* (wood without bark, rotten or not), *fungi* (wood decaying polypore, sap runs), *ivy* (at least on 25% of the tree), *crown* (broken crown, broken main branch or more than 20% of crown is dead wood) and *burls*. Microhabitat diversity and density were assessed on large oak trees in a 20m and a 56m radius around TbT (included). Density of large trees (DBH>70cm) was assessed in the 20m and 56m radius around each trap. We defined the *Openness* as the proportion of canopy openness in a radius of 20m around each trap. All used variables were summarized in Table 2.

Analyses

Our main objectives were to compare (i) species richness and abundance between forest and solitary trees (ii) saproxylic beetle assemblages between forest and solitary trees and (iii) their drivers of such richness and assemblages.

We used a Kruskal-Wallis to test the differences in mean values of environmental variables between forest and solitary trees context.

We used Gaussian or Poisson GLMM (Generalized Liner Mixed Models) to investigate species richness differences between forest or solitary tree contexts on species richness and abundance, with "site" as a spatially-implicit random effect on the intercept (lmer function in lme4 R-package). Since we founded a close correlation between total abundance and the number of beetle species recorded on a plot, we used the number of individuals as a covariate in separate richness models (Gotelli and Colwell, 2001) to separate the effects on the number of individuals from species effects. Some of our traps on solitary tree context were destroyed by weather conditions and do not bring any data on some of three sampling months. Species differs between one sampling months from the other (Nageleisen and Bouget, 2009). We created a corrective factor based on successful traps sampling each month to take into account the missing data when dealing with species richness. We used the log of this corrected factor as an offset in our models. Significance of tested variables on beetles richness or abundance was assessed in forest, solitary or both condition pooled together. We compared the model fit including the tested variable to the model fit without this particular coefficient with a likelihood ratio test to assess his significance.

We performed a spatially constrained ANOSIM with a home-made function to compare species composition between forest and solitary tree contexts.

Using Carvhalo *et al,* (2013) approach, we investigated the assemblage dissimilarity between forest and solitary tree contexts. This approach allows distinguishing the part of total assemblage's dissimilarity due to species replacement (turnover) or richness differences (nestedness).

We used IndVal procedures (DeCaceres and Legendre, 2009), to pull out indicator species of both contexts. We used a 0.05 significance level and 1000 run as parameters.

To rank the effect of the environmental variable among structural predictors on variations in species composition (including singletons), we performed a Canonical Analysis of Principal Coordinates (vegan R-package, CAP, Anderson and Willis, 2003). Based on Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, since co-linearity among predictor variables is not considered to be a problem in CAP.

In the end, we explored the environmental drivers of species (all or rare) richness and abundance between both mixed and separated contexts using GLMM, where "site" was a spatially-implicit random effect on the intercept. Significance of tested environmental drivers on beetles richness or abundance was assessed in forest, solitary using a likelihood ratio test between the models with and without the predictor.

As habitat thresholds are useful to define targets for nature conservation (Müller and Bütler, 2010), we used recursive partitioning (Hothorn and Zeileis, 2008) to search for thresholds in the

significant models related with microhabitat number and diversity. The thresholds are derived from estimates of breakpoints revealed in maximally selected two-sample statistics. Their validity is judged by multiple test procedures. This method provides a decision tree with p-values for one or more critical thresholds. Based on 1000 bootstrap samples, a confidence interval (IC; 95%) was calculated for all thresholds. The significant p-value for thresholds was set at $p<0.01$. Each of the two groups separated by a threshold had to contain at least eight samples to be selected.

All analyses were carried out with the R 3.1.0 (R Core Team, 2013) software.

***Results*:**

Overall, the compiled dataset included 21178 specimens. Among them, 573 beetle's species were identified. A total of 422 species were saproxylic (73%) and represent 13174 individuals (62% of total individuals caught). We found 302 saproxylic species in forest stands and 342 in solitary trees stands. Rare species accounted for 11% in forest and 14% in solitary trees context.

Stand differences between forest and solitary tree context

Among the eleven environmental variable studied, nine were significantly different between tree context (forest or solitary). *Openness* was higher in solitary trees context than in forest tree context (Fig. 1a). As a contrary, deadwood volume was higher in forest than in solitary tree context (Fig. 1b). We observed a higher number (Fig. 1c) and diversity (Fig. 1d) of saproxylic micro-habitats on solitary than on forest TbT's. The number of microhabitats supported by large trees was higher in a 20m radius around the trap in solitary tree context (Fig. 1e), and was not different in a 56m radius around trap (Fig. 1f). Microhabitat diversity was higher in solitary context than in forest tree context, at 20m radius (Fig. 1g) as at a 56m radius (Fig. 1h). The number of tree cavities was higher in solitary tree context than in forest tree context at a 20m radius scale around trap (Fig. 1i). There was no difference in the number large trees in a 20m radius around trap (Fig. 1j). Therefore, there were more large trees at a 56m radius around trap in forest than in solitary context (Fig. 1k). For further details on values, see Tab. 3.

Species richness and abundance between forest and solitary tree context

Nor total or rare species richness, abundance or species richness using the number of individuals as a covariate in separate richness models were significantly different from forest or solitary trees context.

Drivers of species richness and abundance

Forest tree context

In forest context, we did not found any significant driver of total species richness among studied environmental variables (Tab. 4).

Species abundance in forest was positively drived by TbT DBH, (Fig. 2a) and the number of cavities on large trees in a 20m radius around TbT (Fig. 2b).

We did not found any significant driver of species richness when using the number of individuals as a covariate in separate richness models among our environmental variables.

Rare species richness and rare species richness using the number of individuals as a covariate in separate richness models were negatively influenced by the diversity of microhabitats on large trees in a 56m radius around the trap (Fig. 2c), the decrease being lower under a threshold of 2 microhabitats.

Solitary tree context

In solitary tree context only, total species richness was positively influenced by TbT characteristics; TbT DBH (Fig. 3a). Threshold-type relations were found for the diversity of microhabitats born by the TbT (Fig. 3b) and total number of microhabitats born by the TbT (Fig. 3c) effects on total species richness. TbT with a higher number of microhabitats hosted higher species richness. The increase in species number was important before a threshold of 4 microhabitats (IC, 1;4). When TbT microhabitat diversity was over 3 (IC; 0;4), species accumulation curve was slightly decreasing, but with very high sd values. All other environmental variables did not significantly influence total species richness.

Total species abundance was not significantly influenced by TbT DBH. Therefore, both TbT microhabitat number (Fig. 3d) and diversity (Fig. 3e) significantly influence all species abundance, with threshold-type relations. Individuals abundance accumulation rate was higher before the a threshold of 3 microhabitats number (IC, 1;6). Accumulation rate was similar between and after the threshold of 2 microhabitats diversity for abundance accumulation rate (IC, 1;4). An increase in microhabitat diversity in a 56m radius positively affects total species abundance (Fig.3f) without detected threshold. All other environmental variables did not show any significant response.

In solitary tree context only, rare species richness was positively influenced by TbT microhabitat number (Fig. 4a) and diversity (Fig. 4b) in threshold-types relations. We observe an increase in rare species richness after a threshold of 4 microhabitats per TbT (IC, 1;6), and a slight decrease after a threshold of 3 microhabitat types (IC, 1;4). Also, microhabitat diversity in a 56m radius significantly affects rare species richness, in a threshold-type relation. After a threshold of 3 (IC, 2;4) microhabitat types, rare species richness accumulation rate strongly increases (Fig. 4c). All other environmental variables did not show any significant response.

Rare species abundance was significantly influenced by TbT diversity of microhabitats (Fig. 4d). The individuals accumulation rate was therefore constant before and after a threshold of 1 microhabitat (IC, 0;4). Stand openness was also a significant driver of rare species abundance (Fig. 4e).

Species assemblage's between forest and solitary trees

a) ANOSIM (All species, rare species)

A spatially constrained ANOSIM revealed significant species assemblages between forest and solitary trees context's, for both all and rare species ($p<0.001$).

b) Dissimilarity approach (All species, rare species)

All species assemblages mean dissimilarity was about 0.47. Most of the dissimilarity was due to species turnover between forest and solitary trees conditions (90%, Tab. 5). For rare species, assemblages mean dissimilarity was higher, about 0.62. As for all species, the largest part of total dissimilarity was due to species replacement (92%, Tab. 6). For all and rare species, the remaining 10% of dissimilarity were explained by nestedness, *i.e* supplementary species in one or the other assemblage.

c) Indicator species for forest or solitary tree context (All species, rare species)

Without indicator value restriction and using only the p-value (< 0.05) as a species indicator selection, we found 81 indicator species, 42 for forest tree context and 39 for solitary tree context (Tab. 7). Most of species had very low indicative power but are highly significant. For rare species, three characteristic species for forest and three for solitary tree context were set out by the analyses. There were *Calambus bipustulatus* (Elateridae), *Isorhipis marmottani* (Eucnemidae) and *Trichoceble floralis* (Dasytidae) for forest context and *Pedostragalia revestita* (Cerambycidae), *Procraerus tibialis* (Elateridae) and *Brachygonus ruficeps* (Elateridae) for solitary trees context.

Drivers of species assemblages

Forest

In forest context only, *Openness* was the only driver of total species assemblages (3.90% of total inertia explained) among variables we used. No one of our variables was relevant for forest rare species assemblages (Tab. 8).

Solitary

In solitary tree context, TbT characteristics were the main variables driving total species assemblages. The most explanative one was the TbT DBH (4.23% of total inertia explained). Also, the total number of cavities on large trees in a radius of 20m around TbT and the diversity of microhabitats on large trees in a radius of 20m around trap were significant drivers of total species assemblages.

For rare species, the number, diversity of TbT microhabitats and the diversity of microhabitats on large trees in a radius of 20m or 56m around trap were relevant drivers of species assemblages. The two most explanative factors were the diversity of TbT microhabitats and diversity of microhabitats in a 56m radius around trap (5.25% of total inertia explained).

***Discussion*:**

Forest and solitary tree characteristics

We highlighted major structural differences between forest and solitary trees contexts. Openness was logically higher around solitary tree than forest trees. Also, deadwood volume was higher in forest than in solitary tree context. In contrary, the number and diversity of microhabitats were higher on solitary than on forest TbT's. Mean microhabitat density per tree in 1ha stands was not different between forest and solitary tree contexts. However, microhabitat diversity was greater on solitary trees than in forest context.

Influence of context on saproxylic beetle assemblages associated to large oaks

Are saproxylic beetle assemblages affected by the forest/solitary context?

According to our results, richness was not different between forest and solitary trees contexts. Different species were hold by each oak tree context. We observe a similar trend (highly significant ANOSIM), with about 50% dissimilarity assemblages between forest and solitary trees context. About 90% of this dissimilarity was due to species turnover rather than species nestedness. We detect a large number of significant common indicator species for each of the studied tree contexts, even if their indicator value was low. In a Norway forest and solitary oak study, Sverdrup-Thygesson *et al,* (2010) founded consistent results. They found no differences in total species richness, and 50% dissimilar assemblages between forest and solitary trees. Both contexts sustained specific species. Oleksa and Gawronski (2006) found two red listed beetles *Osmoderma eremita* and *Protaetia marmorata* to be solitary trees specialists, and being negatively impacted by an increase of forest in surrounding landscape. In our data, *Protaetia marmorata* was encountered in forest as in solitary trees. However, we found another large Cetoniidae species *Cetonischema aeruginosa* to be a significant solitary tree specialist.

Rare species

In our solitary trees dataset, 14% of species were rare species. Neither rare species richness nor abundance differences were found between both contexts. As for all species, rare species assemblages between forest and solitary tree context were 50% shared. A total of tree rare species were founded as specialist in each context. Rare species proportions in solitary trees seemed to be constant across Europe, as Sverdrup-Thygesson (2009) in Norway, Horak (2014) in Czech Republic, and Jonsell (2012) in Sweden founded same proportion of rare species in their data. Half shared rare species number between forest and solitary trees results are supported by Sverdrup-Thygesson *et al,* (2010). Rare indicators species were far less numerous than common species, as it's generally observed (Schiegg, 2000). Among the three rare indicators species of each context, *Calambus bipustulatus* (Elateridae) was also pointed out by Bergmann *et al,* (2012) as a forest specialist.

Are key drivers for saproxylic biodiversity the same in forest vs solitary contexts?

Key drivers for saproxylic beetles biodiversity were not consistent between forest and solitary tree contexts. Few drivers of species richness or assemblages were found in forest context. In contrary, total or rare species richness were strongly influenced by all TbT variables. Solitary tree species assemblages were also driven by several TbT characteristics. Rare species assemblages were also structured by one of the TbT's characteristics. Note that forest dead wood volume was not a significant driver of species richness, abundance or composition. This supports Lassauce *et al,* (2011) results.

Several studies emphasis the importance of stand openness as a saproxylic beetle driver (Jonsell *et al.,* 1998; Horak *et al.,* 2014), in particular in Oak forests (Horak and Rebl, 2013). However, in solitary tree context, TbT characteristics were the main drivers of species (all and rare) assemblages, openness did not seems to play any significant role. The low variations in openness around solitary trees may not be a relevant variable for species assemblages. Sverdrup-Thygesson *et al,* (2010) founded the DBH of support tree to be one of the main drivers of red-listed species. In our data, the DBH of TbT was not a significant driver of rare species richness. This may be due to a low range in TbT values, and similar TbT DBH's between forest and solitary tree contexts. However, the number and diversity of microhabitats on TbT had a positive influence on rare species richness. Microhabitats are known to be valuable for saproxylic beetles local species richness (Bouget *et al.,* 2014; Larrieu, 2014).

Solitary trees at stake for biodiversity conservation

Solitary and forest trees supported the same number of saproxylic beetle species (Jonsell, 2012), but only a half of them were shared (Sverdrup-Thygeson *et al.,* 2010; Jonsell, 2012). This indicates a strong refuge value for saproxylic beetles for both elements and for biodiversity in general (Fischer *et al.,* 2010). Solitary trees are slowly disappearing (Orlowski and Nowak, 2007). This is partly due to private owner, who, in order to facilitate crop work with large engines removes them, even if solitary trees does not impact crop production (Rivesta *et al.,* 2013). Another threat to solitary trees –and associated biodiversity- is forest regrowth. Forest regrowth was found to be detrimental for many beetle species inhabiting on solitary trees (Ranius and Jansson, 2000). Solitary trees sustained a large number of species providing benefits for agriculture (like bees, Lentini *et al.,* 2012), but not only. They hold solitary tree specialist species and some of them are of prior conservation interest, like the protected red-listed beetle *Osmoderma eremita*. They have a high conservation value as stepping stones for saproxylic biodiversity in nowadays highly fragmented agricultural or urban landscapes (Alvey, 2006; Saville *et al.,* 1997).

There is an urgent need for public policies to better take into account such structures, as forests alone cannot support the whole saproxylic biodiversity. They must be aware that unique conservation strategy is not enough to ensure their conservation (Schirmer *et al.,* 2012).

Should forest habitat trees mimic solitary trees?

We found solitary trees to be of high importance for saproxylic beetle conservation, in particular for rare species. Tree DBH, microhabitat number and diversity as stand openness were

founded to be major drivers of species richness and composition. Moreover, solitary TbT associated species richness was related to microhabitat number and diversity thresholds, allowing concrete management recommendations (Müller and Bütler, 2010) for habitat tree selection. Solitary trees are managed in a different way than forest trees (Sebek *et al.,* 2013). This particular management – pollarding for example- allows a fast microhabitat creation, in particular cavities. Cavities are one of the most important micro-habitats for saproxylic biodiversity, and one of the most studied (Kraus and Krumm, 2013). View the fact that in managed forest stands, trees support less microhabitats than in reserve ones (Bouget *et al.,* 2014; Winter and Möller, 2008; Larrieu and Cabanettes, 2012) and our forest stands were managed stands, we can suppose that total microhabitat number per Ha could be higher in natural forest than in solitary trees stands. Habitat active creation (Abrahamson *et al.,* 2009; Ehnström, 2001) may not be needed to ensure sufficient densities of microhabitat bearing trees in forest, if sufficient well choosed habitat trees are set in place. Stand openness around such trees must be enhanced (Widerberg *et al.,* 2012) but with great care (Franc and Götmark 2008) as it could also have negative effects on other saproxylic organisms (Norden *et al.,* 2008).

Conclusions and perspectives

Our study provides elements promoting solitary tree conservation, and strongly sustains the green tree retentions practices at final harvesting (Gustafsson *et al.,* 2010). Forest managers should focus on microhabitat bearing trees retention at final harvesting. But saproxylic beetles conservation not only relies on forests. Public policies should promote such solitary elements in both agricultural and urban landscapes.

As solitary trees are slowly disappearing (Orlowski, 2007), nowadays assemblages may be 'living dead' populations (Kraus and Krumm, 2013; Kuussaari *et al.,* 2009). Past structure of landscape distribution habitat can have influences on nowadays species assemblages (Ranius *et al.,* 2008). Further studies should explore the past landscape effects on solitary trees species assemblages. Also, the role of solitary trees as stepping stones should be explored to determine how and at what scale they are used as relays between forests.

Acknowlodgments:

We are grateful to Carl Moliard for field assistance, Thierry Noblecourt (Scolytidae), Fabien Soldati (Tenebrionidae), Thomas Barnouin (Elateridae, Ptinidae (excl. Ptininae)), Olivier Rose and Bernard Moncoutier (Ciidae, Lathridiidae, Cryptophagidae, Leiodidae), Philippe Millarakis (Histeridae), Christian Perez (Pselaphidae, Scydmaenidae), Gianfranco Liberti (Dasytidae, Malachidae, Cantharidae) and Benjamin Calmont (Ptininae) for specimen identification. Thanks to the involved forest national office agents for their strong implication in getting authorizations to private owners and municipalities. We are grateful to private landowners and towns which authorized the sampling on their fields and forests.

References

Abrahamsson, M., Jonsell. M., Niklasson. M., Lindbladh. M., (2009). Saproxylic beetle assemblages in artificially created high-stumps of spruce (Picea abies) and birch (Betula pendula ⁄ pubescens) – does the surrounding landscape matter? *Insect Conservation and Diversity* **2**, 284–294.

Alexander, K.N.A., (2008). Tree biology and saproxylic coleopteran: Issues of definitions and conservation language. *Rev. Écol. (Terre Vie)* **63**: 1-5.

Alvey, A.A., (2006). Promoting and preserving biodiversity in the urban forest. *Urban Forestry and Urban Greening* **5**: 195–201.

Anderson, M.J., Willis. T.J., (2003). Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* **84**:511–525.

Bergmann, K.O., Jansson, N., Claesson, K., Palmer, M.W., Milberg, P., (2012). How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. *Forest Ecology and Management* **265**: 133–141.

Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., (2013). In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation* **22**: 2111–2130.

Bouget, C., Larrieu, L., Brin, A., (2014). Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators* **36**: 656–664.

Carvalho, J.C., Cardoso, P., Borges, P.A.V., Schmera, D., Podani, J., (2013). Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches. *Oikos* **122**: 825–834.

De Caceres, M., Legendre, P., (2009). Associations between species and groups of sites: indices and statistical inference. Ecology, URL http://sites.google.com/site/miqueldecaceres/

Dubois, G.F., Vignon, V., Delettrec, Y.R., Rantierc, Y., Vernona,P., Burel, F., (2009).Factors affecting the occurrence of the endangered saproxylic beetle *Osmoderma eremita* (Scopoli, 1763) (Coleoptera: Cetoniidae) in an agricultural landscape. *Landscape and Urban Planning* **91**: 152–159.

Enshtröm, B., (2001). Leaving Dead Wood for Insects in Boreal Forests - Suggestions for the Future. *Scandinavian Journal of Forest Research* **16**, 91-98.

Fischer, J., Stott, J., Law, B.S., (2010). The disproportionate value of scattered trees. *Biological conservation* **143**: 1564-1567

Franc, N., Götmark, F., (2008). Openness in management: Hands-off vs partial cutting in conservation forests, and the response of beetles. *Biological conservation* **141**: 2310-2321.

Gotelli, N.J., Colwel, R.K., (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**: 379-391.

Grove, S.J., (2002). Saproxylic Insect Ecology and the Sustainable Management of Forests. *Annual Review of Ecology and Systematics* **33**: 1-23.

Gustafsson, L., Kouki, J., Sverdrup-Thygeson, A., (2010). Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. *Scandinavian Journal of Forest Research* **25**: 295-308.

Hector, A., Bagchi, R., (2007). Biodiversity and ecosystem multifunctionality. *Nature* **448**: 188–191.

Horak, J., (2014). Fragmented habitats of traditional fruit orchards are important for dead wood-dependent beetles associated with open canopy deciduous woodlands. *Naturwissenschaften* **101**:499–504.

Horak, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P., Pech, P., (2014). Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. *Forest Ecology and Management* **315**: 80–85.

Horak, J., Rébl. K., (2013). The species richness of click beetles in ancient pasture woodland benefits from a high level of sun exposure. *Journal of Insect Conservation* **17**:307–318.

Hothorn, T., Zeileis, A., (2008). Generalized maximally selected statistics. Biometrics 64, 1263-1269.

Jansson, N., Coskun, M., (2008). How similar is the saproxylic beetle fauna on old oaks (Quercus spp.) in Turkey and Sweden? *Revue Écologie (Terre Vie)* **63**: 83-91.

Jonsell, M., (2004). Old park trees: a highly desirable resource for both history and beetle diversity. *Journal of Arboriculture* **30**: 238-244.

Jonsell, M., (2012). Old park trees as habitat for saproxylic beetle species. *Biodiversity and Conservation* **21**:619–642.

Jonsell, M., Weslien, J., Ehnström, B., (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation* **7**: 749-764.

Kraus, D., Krumm, F. (eds) (2013). *Integrative approaches as an opportunity for the conservation of forest biodiversity.* European Forest Institute. 284 pp.

Kuussaari, M., Bommarco, R., Heikkinen, R., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., Ingolf, S.D., (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* **24**: 564-571.

Larrieu, L., (2014). *Les dendro-microhbitats: facteurs clés de leur occurrence dans les peuplements forestiers, impact de la gestion et relations avec la biodiversité taxonomique.* Université de Toulouse, Doctoral thesis : 115p.

Larrieu, L., Cabanettes, A., (2012). Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests. *Canadian Journal of Forest Research* **42**: 1433–1445.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., (2011). Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators* **11**: 1027–1039.

Lentini, P.E., Martin, T.G., Gibbons, P., Fischer, J., Cunningham, S.A., (2012). Supporting wild pollinators in a temperate agricultural landscape: Maintaining mosaics of natural features and production. *Biological conservation* **149**: 84-92.

Manning, A.D., Fischer, J., Lindenmayer, D.B., (2006). Scattered trees are keystone structures – Implications for conservation. *Biological conservation* **132**: 311-321.

Matveinen-Huju, K., Niemela, J., Rita, H., O'Hara, R.B., (2006). Retention-tree groups in clear-cuts: Do they constitute 'life-boats' for spiders and carabids? *Forest Ecology and Management* **230**: 119-135.

Müller, J., Bütler, R., (2010). A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research* **129**:981–992.

Nageleisen, L.M., Bouget, C., (Eds) (2009). *L'étude des insectes en forêt : méthodes et techniques, éléments essentiels pour une standardisation*. Synthèse des réflexions menées par le groupe de travail « Inventaires Entomologiques en Forêt » (Inv.Ent.For.). Les Dossiers Forestiers n°19, Office National des Forêts, 144 p.

Nieto, A., Alexander, N.A., (2010). *European RedList of saproxylic beetles*. Luxembourg: Publications Office of the European Union. 39p.

Nordén, B., Götmark, F., Ryberg, M., Paltto, H., Allmér, J., (2008). Partial cutting reduces species richness of fungi on woody debris in oak-rich forests. *Canadian Journal of Forest Research* **38**: 1807–1816.

Oleksa, A., Gawronski, R., (2006). Forest in an agricultural landscape – presence of old trees is more important than the existence of nearby forest. *Ecological questions* **7**: 29-36.

Orłowski, G., Nowak, L., (2007). The importance of marginal habitats for the conservation of old trees in agricultural landscapes. *Landscape and Urban Planning* **79**: 77-83.

Palm, T., (1959). Die Holz- und Rindenkäfer des süd- und mittelscwedischen Laubbäume. *Opuscula Entomologica Supplementum* **16**: 1-374.

R Core Team., (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ranius, T., Nilsson, S.G., (1997). Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees. *Journal of Insect Conservation* **1**: 193–204.

Ranius, T., Jansson, N., (2000). The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation* **95**: 85-94.

Ranius, T., Johansson, P., Eliasson, P., (2008). Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. *Biodiversity and Conservation* **17**: 2371–2381

Ranius, T., Jansson, N., (2000). The influence of forest re-growth, original canopy cover and tree size on saproxylic beetles associated with old oaks *Biological Conservation* **95**: 85–94.

Rivesta, D., Paquetta, A., Morenob, G., Messiera, C., (2013). A meta-analysis reveals mostly neutral influence of scattered trees on pasture yield along with some contrasted effects depending on functional groups and rainfall conditions. *Agriculture, Ecosystems and Environment* **165**: 74– 79.

Sahlin, E., Schroeder, L.M., (2010). Importance of habitat patch size for occupancy and density of aspen-associated saproxylic beetles. *Biodiversity and Conservation* **19**:1325–1339.

Saville, N.M., Dramstad, W.E., Fry, G.L.A., Corbet, S.A., (1997) Bumblebee movement in a fragmented agricultural landscape. *Agriculture, Ecosystems and Environment* **61**: 145-154.

Schiegg, K., (2000). Are there saproxylic beetle species characteristic of high dead wood connectivity? *Ecography* **23**: 579-587.

Schrimer, J., Dovers, S., Clayton, H., (2012). Informing conservation policy design through an examination of landholder preferences: A case study of scattered tree conservation in Australia. *Biological Conservation* **153**: 51–63.

Sebek, P., Altman, J., Platek, M., Cizek, L., (2013). Is Active Management the Key to the Conservation of Saproxylic Biodiversity? Pollarding Promotes the Formation of Tree Hollows. *PLoS ONE* **8**: e60456. doi:10.1371/journal.pone.0060456

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management* **128**, 211–225.

Sverdrup-Thygeson, A., Skarpaas, O., Ødegaard, F., (2010). Hollow oaks and beetle conservation: the significance of the surroundings. *Biodiversity and Conservation* **19**:837–852.

Sverdrup-Thygeson, A., (2009). *Oaks in Norway: Hotspots for red-listed beetles (Coleoptera).* In: Buse, J., Alexander, K.N.A., Ranius, T., Assmann, T. (Eds). *Saproxylic beetles – Their role and diversity in European woodland and tree habitats.* Proceedings of the 5th Symposium and Workshop on the Conservation of saproxylic Beetles. Pensoft, Sofia-Moscow, 235p.

Tscharntke, T., Steffan-Dewenter, I., Krues, A., Thies, C., (2002). Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research* **17**: 229–239.

Vodka, S., Konvicka, M., Cizek, L., (2009). Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *Journal of Insect Conservation* **13**: 553–562.

Widerberg, M.K., Ranius, T., Drobyshev, I., Nilsson, U., Lindbladh, M., (2012). Increased openness around retained oaks increases species richness of saproxylic beetles. *Biodiversity and Conservation* **21**: 3035-3059.

Winter, S., Möller, G.C., (2008). Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management* **255**: 1251–1261.

Figures

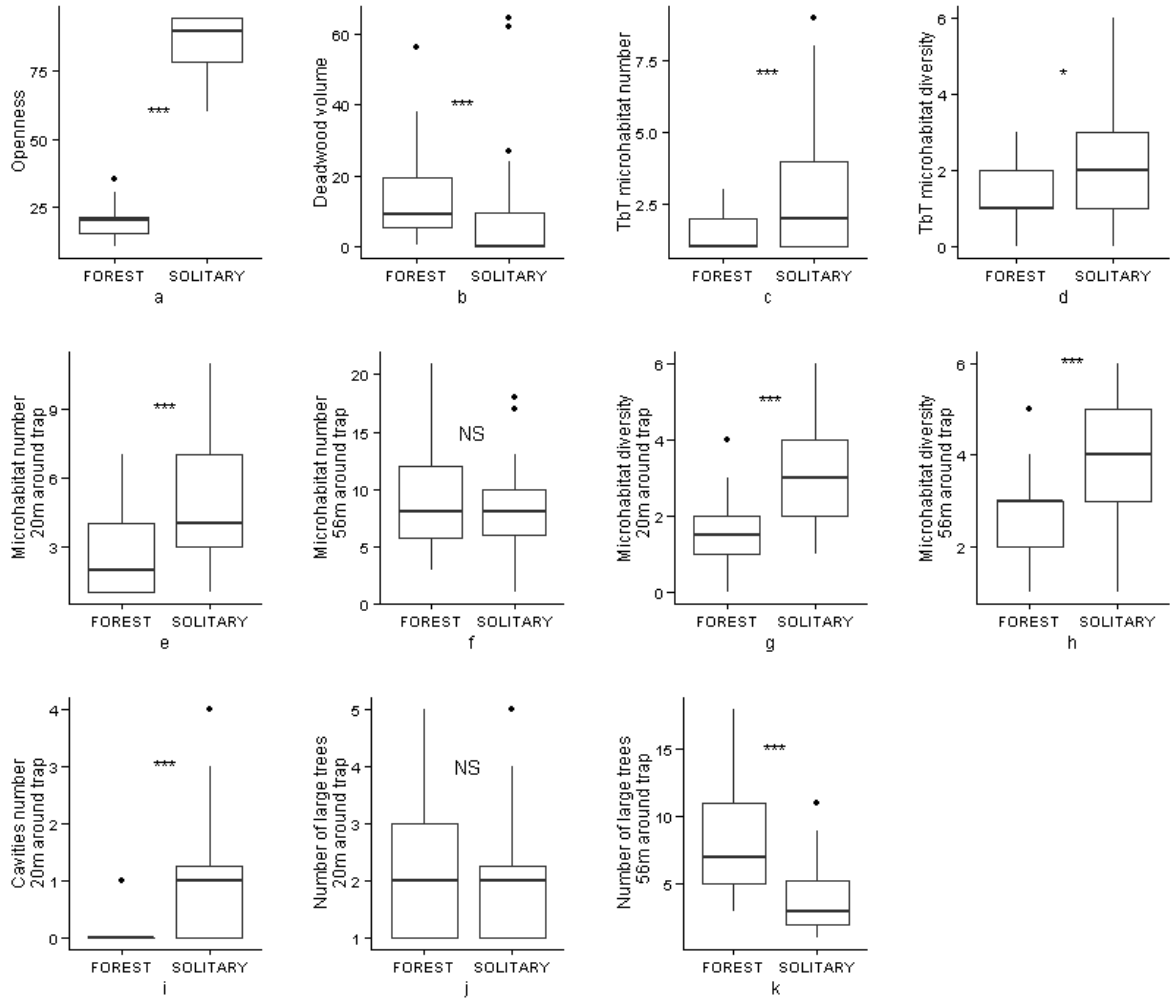


Figure 1 (a to k): Environmental variable differences between forest and solitary trees context. Bars in boxplots are the median. Differences in mean values were assessed with Kruskal-Wallis test. Signif codes: (*** p<0.001, ** 0.01>p>0.001, * 0.05>p>0.01 NS: non-significant).

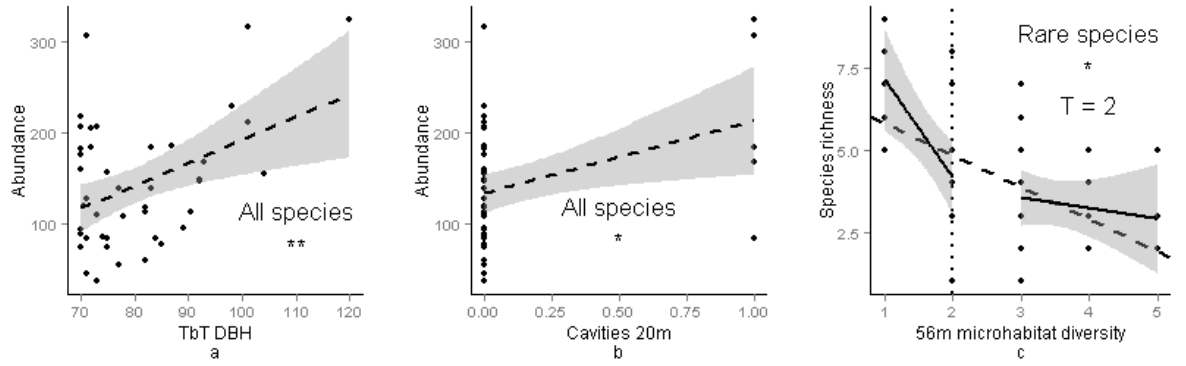


Figure 2 (a to c): significant relations between total species abundance and environmental variables in forest context. Dashed line: species accumulation rate. Continuous line: species accumulation rate before and after threshold (vertical line, T = threshold). The grey areas are the standard deviation of the accumulation rate curves. They are represented on the global species accumulation rate when no threshold appears, and on species accumulation rate before and after threshold lines when a threshold occurs. Signif codes: (*** p<0.001, ** 0.01>p>0.001, * 0.05>p>0.01)

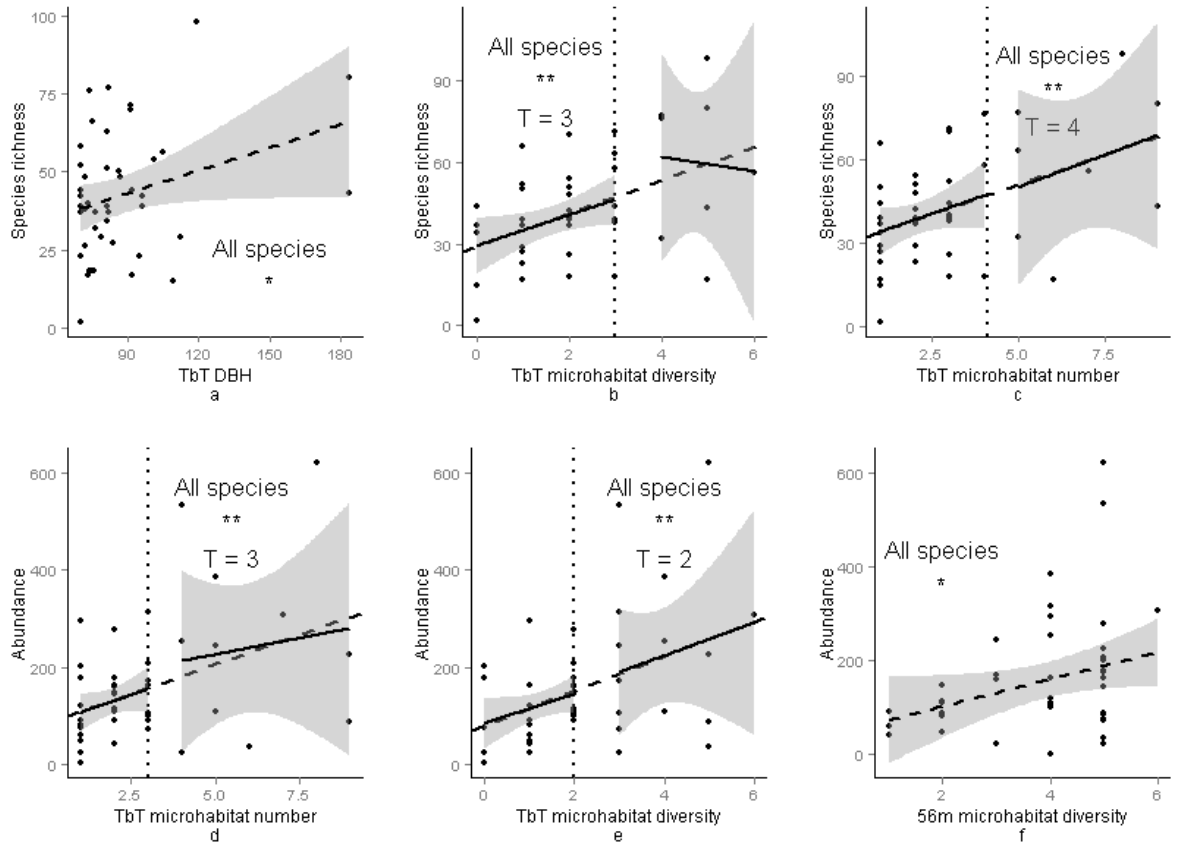


Figure3 (a to f): Significant relations between total species richness or abundance and environmental variables in solitary trees context. Dashed line: species accumulation rate. Continuous line: species accumulation rate before and after threshold (vertical line, T = threshold). The grey areas are the standard deviation of the accumulation rate curves. They are represented on the global species accumulation rate when no threshold appears, and on species accumulation rate before and after threshold lines when a threshold occurs. Signif codes: (*** p<0.001, ** 0.01>p>0.001, * 0.05>p>0.01)

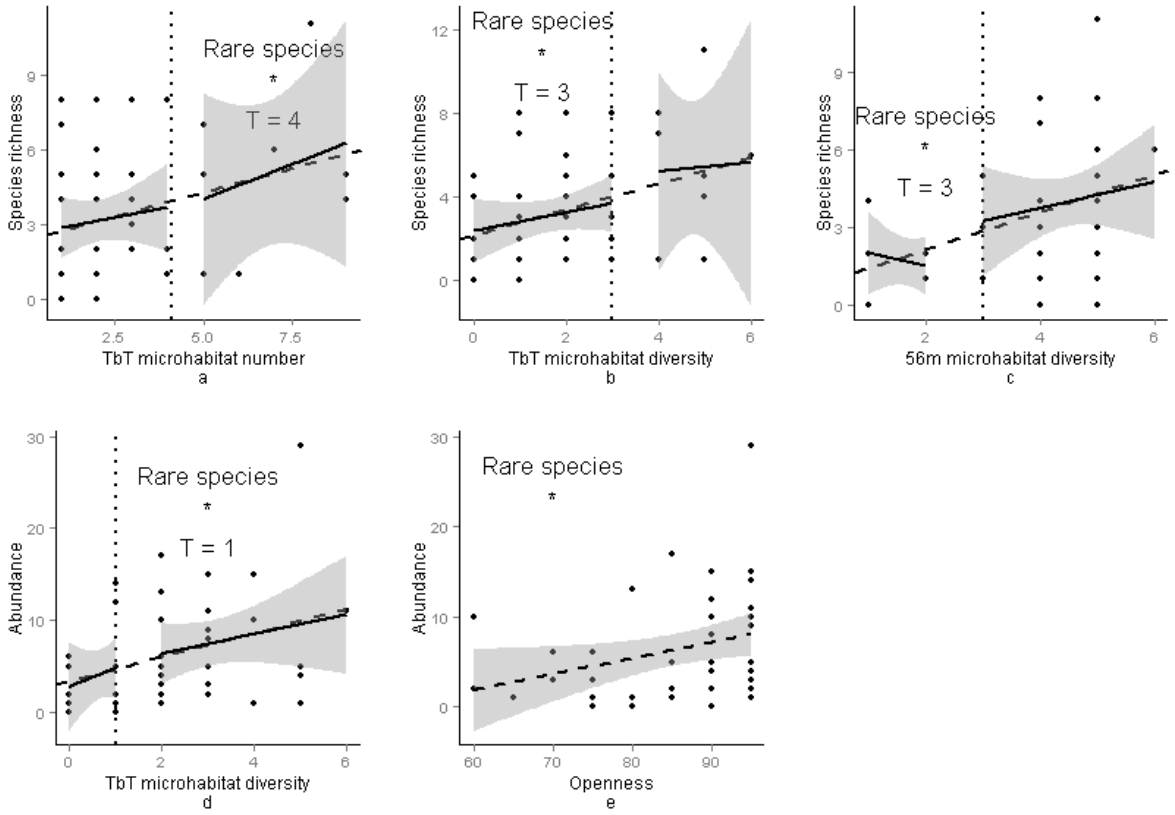


Figure 4 (a to e): significant relationship between rare species richness or abundance and environmental variables in solitary trees context. Dashed line: species accumulation rate. Continuous line: species accumulation rate before and after threshold (vertical line, T = threshold). The grey areas are the standard deviation of the accumulation rate curves. They are represented on the global species accumulation rate when no threshold appears, and on species accumulation rate before and after threshold lines when a threshold occurs. Signif codes: (*** p<0.001, ** 0.01>p>0.001, * 0.05>p>0.01)

Tables

	Forest	Solitary	Total
MARCENAT (03)	9	11	20
MARLY-LE-ROI (78)	8	8	16
RAMBOUILLET (78)	10	9	19
SOUVIGNY (03)	9	10	19
YZEURE (03)	8	6	14
Total	44	44	88

Table 1 : Trap repartition.

Variable	Description
FOREST	Name of the forest or private area with solitary trees
Tree context	Trap context: forest tree or solitary tree
BMT	Total volume of dead wood
TbT DBH	Trap bearing Tree Diameter at Breast Height
TbT microhabitat number	Trap bearing Tree number of microhabitats. We consider seven different types of microhabitats: cavities (empty, woodpecker holes, dendrothelms…), bark (bark detachment, crack in the trunk), visible wood (wood without bark, rotten or not), fungi (wood decaying polypore, sap runs), ivy (at least on 25% of the tree), crown (broken crown, broken main branch or more than 20% of crown is dead wood) and burls.
TbT microhabitat diversity	Trap bearing Tree diversity of microhabitats.
nbcav20	Total numbers of cavities supported by large trees in a radius of 20m around TbT. Cavities supported by the TbT are included.
nbmh20	Total numbers of microhabitats supported by large trees in a radius of 20m around TbT. Microhabitats supported by the TbT are included.
nbmh56	Total numbers of microhabitats supported by large trees in a radius of 56m around TbT. Microhabitats supported by the TbT are included.
divmh20	Total type numbers of microhabitats supported by large trees in a radius of 20m around TbT. Microhabitats supported by the TbT are included.
divmh56	Total type numbers of microhabitats supported by large trees in a radius of 56m around TbT. Microhabitats supported by the TbT are included.
Openness	Canopy openness estimated by single operator in a 20m radius around the Trap bearing Tree.
nbtree>7020m	Total number of trees with DBH>70cm in a 20m radius around the Trap bearing Tree. The Trap bearing tree is included.
nbtree>7056m	Total number of trees with DBH>70cm in a 56m radius around the Trap bearing Tree. The Trap bearing tree is included.
SRtot	Saproxylic beetle species richness per trap
ABtot	Saproxylic beetle abundance per trap
SRrar	Rare saproxylic beetle species richness per trap
ABrar	Rare saproxylic beetle abundance per trap

Table 2: Environmental variables used in the analyses.

	Forest (SD)	Isolated (SD)	Kruskal test p-value	Signif
NbMH_ArbPort	1.409091 (0.6220066)	2.954545 (2.156165)	1.74E-05	***
DivMH_ArbPort	1.295455 (0.7014784)	2.204545 (1.533798)	0.002453	**
Openness	19.77273 (5.999471)	85.22727 (10.72676)	3.72E-16	***
nbcav20	0.1136364 (0.3210382)	1.068182 (1.06526)	8.79E-08	***
nbmh20	2.704545 (1.811841)	4.863636 (2.664067)	7.95E-05	***
nbmh56	9.340909 (4.477038)	8.090909 (3.690454)	0.2983	ns
divmh20	1.704545 (0.9783599)	3.159091 (1.445815)	3.044E-06	***
divmh56	2.75 (1.102323)	3.886364 (1.333223)	4.81E-05	***
nbtree.7020m	2.204545 (1.339551)	1.931818 (1.108062)	0.4294	ns
nbtree.7056m	8.181818 (4.25508)	3.863636 (2.416907)	9.77E-08	***
VBMT	13.81875 (11.66841)	7.390645 (14.32794)	1.17E-05	***

Table 3: Environmental and stand characteristic from Forest or solitary tree contexts.

	Forest						Solitary					
	Total species richness			Rare species richness			Total species richness			Rare species richness		
	Abond	RS	RS~log(Abond)	Abond	RS	RS~log(Abond)	Abond	RS	RS~log(Abond)	Abond	RS	RS~log(Abond)
BMT	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
DBH_ArbPort	**	ns	ns	ns	ns	ns	ns	*	**	ns	ns	
NbMH_ArbPort	ns	ns	ns	ns	ns	ns	**	**	**	ns	*	
DivMH_ArbPort	ns	ns	ns	ns	ns	ns	**	**	*	*	*	
nbcav20	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
openess	ns	ns	ns	ns	ns	ns	ns	ns	*	*	ns	
nbmh20	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
nbmh56	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
divmh20	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
divmh56	ns	ns	ns	ns	*	*	*	ns	ns	ns	*	
nbtrees.7020m	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
nbtrees.7056m	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	

Table 4: Context and environmental variables effects on species richness and abundance.

	Species nestedness	Species turnover	Total dissimilarity	% species replacement from total dissimilarity
Marly	0.01	0.37	0.39	96.63
Rambouillet	0.02	0.40	0.42	95.11
Yzeure	0.06	0.51	0.57	89.33
Souvigny	0.06	0.46	0.52	88.00
Marcenat	0.07	0.42	0.49	85.41
mean	**0.05**	**0.43**	**0.48**	**90.43**

Table 5: Dissimilarity partitioning results for all species.

	Species nestedness	Species turnover	Total dissimilarity	% species replacement from total dissimilarity
Marly	0.08	0.50	0.58	86.36
Rambouillet	0.03	0.67	0.70	95.65
Yzeure	0.06	0.60	0.66	91.30
Souvigny	0.02	0.74	0.76	97.45
Marcenat	0.05	0.38	0.43	87.50
mean	**0.05**	**0.58**	**0.62**	**92.33**

Table 6: Dissimilarity partitioning results for rare species.

Forest Species	Context	Indicator value	probability	Solitary tree Species	Context	Indicator value	probability
Melanotus_villosus	Forest	0.767	0.001	*Abdera_bifasciata*	Solitary	0.7609	0.001
Cerylon_ferrugineum	Forest	0.6589	0.001	*Euglenes_oculatus*	Solitary	0.472	0.001
Calambus_bipustulatus	**Forest**	**0.6555**	**0.001**	*Megatoma_undata*	Solitary	0.4679	0.001
Mycetochara_maura	Forest	0.6097	0.01	*Grammoptera_ustulata*	Solitary	0.3826	0.001
Nalassus_laevioctostriatus	Forest	0.5988	0.001	*Magdalis_flavicornis*	Solitary	0.3612	0.005
Ptinus_subpillosus	Forest	0.5649	0.001	*Cis_pygmaeus*	Solitary	0.3387	0.004
Stenagostus_rhombeus	Forest	0.5474	0.001	*Cryptolestes_duplicatus*	Solitary	0.3157	0.011
Rhizophagus_bipustulatus	Forest	0.5448	0.001	*Gastrallus_laevigatus*	Solitary	0.3068	0.001
Ampedus_quercicola	Forest	0.5337	0.002	*Atomaria_fuscata*	Solitary	0.3023	0.001
Enicmus_rugosus	Forest	0.5213	0.02	*Dorcatoma_flavicornis*	Solitary	0.2955	0.001
Isorhipis_marmottani	**Forest**	**0.5191**	**0.001**	*Globicornis_nigripes*	Solitary	0.2855	0.001
Dacne_bipustulata	Forest	0.5092	0.035	*Ptinus_sexpunctatus*	Solitary	0.2775	0.002
Cortodera_humeralis	Forest	0.4786	0.003	*Axinotarsus_marginalis*	Solitary	0.2727	0.001
Ampedus_nigerrimus	Forest	0.4688	0.001	*Dermestes_lardarius*	Solitary	0.2727	0.002
Hemicoelus_costatus	Forest	0.4157	0.001	***Pedostrangalia_revestita***	**Solitary**	**0.2727**	**0.001**
Ampedus_pomorum	Forest	0.3825	0.001	*Tetrops_praeustus*	Solitary	0.2727	0.001
Melasis_buprestoides	Forest	0.3771	0.021	*Dorcatoma_chrysomelina*	Solitary	0.25	0.001
Litargus_connexus	Forest	0.3455	0.002	*Atomaria_linearis*	Solitary	0.2453	0.042
Cetonia_aurata	Forest	0.3209	0.006	*Sphinginus_lobatus*	Solitary	0.2441	0.012
Latridius_hirtus	Forest	0.3182	0.001	*Hylastinus_obscurus*	Solitary	0.2368	0.001
Plegaderus_dissectus	Forest	0.3037	0.008	*Corticarina_minuta*	Solitary	0.2361	0.003
Cryptophagus_scanicus	Forest	0.2871	0.042	*Cryptarcha_undata*	Solitary	0.2345	0.039
Cis_fusciclavis	Forest	0.2833	0.033	*Alphitobius_diaperinus*	Solitary	0.2273	0.005
Anisotoma_humeralis	Forest	0.2668	0.05	*Dasytes_aeratus*	Solitary	0.2182	0.025
Aspidiphorus_lareyniei	Forest	0.2654	0.029	*Trox_scaber*	Solitary	0.2159	0.015
Cis_micans	Forest	0.2392	0.006	*Dasytes_plumbeus*	Solitary	0.2143	0.003
Platystomos_albinus	Forest	0.2368	0.002	***Procraerus_tibialis***	**Solitary**	**0.2066**	**0.006**
Ennearthron_cornutum	Forest	0.2364	0.014	*Eulagius_filicornis*	Solitary	0.2059	0.036
Rutpela_maculata	Forest	0.2251	0.012	*Mesocoelopus_niger*	Solitary	0.2045	0.003
Corticaria_serrata	Forest	0.2045	0.003	*Dermestes_bicolor*	Solitary	0.1818	0.007
Tillus_elongatus	Forest	0.202	0.016	*Protaetia_cuprea*	Solitary	0.1818	0.007
Aplocnemus_impressus	Forest	0.186	0.019	*Malthinus_frontalis*	Solitary	0.1805	0.039
Alosterna_tabacicolor	Forest	0.1818	0.006	*Atomaria_nigrirostris*	Solitary	0.1688	0.028
Bibloporus_mayeti	Forest	0.1731	0.036	*Anobium_punctatum*	Solitary	0.1591	0.015
Platycerus_caraboides	Forest	0.1711	0.029	*Abdera_quadrifasciata*	Solitary	0.1477	0.045
Bibloporus_minutus	Forest	0.1591	0.018	*Orthocis_coluber*	Solitary	0.1414	0.05
Coxelus_pictus	Forest	0.1591	0.011	*Protaetia_aeruginosa*	Solitary	0.1364	0.017
Microrhagus_pygmaeus	Forest	0.1591	0.012	*Prionychus_ater*	Solitary	0.125	0.05
Trichoceble_floralis	**Forest**	**0.1591**	**0.016**	***Brachygonus_ruficeps***	**Solitary**	**0.1136**	**0.049**
Hylis_simonae	Forest	0.1458	0.044				
Anoplodera_sexguttata	Forest	0.1364	0.027				
Platydema_violaceum	Forest	0.1364	0.02				

Table 7: Indicator species returned by the IndVal analyses. Rare species are in bold.

		All species			Rare species		
		Total contribution to inertia			Total contribution to inertia		
		Var	%	signif	Var	%	signif
Forest	BMT	0.29	2.77	ns	0.34	3.3	ns
	DBH_ArbPort	0.3	2.81	ns	0.34	3.34	ns
	NbMH_ArbPort	0.31	2.89	ns	0.27	2.58	ns
	DivMH_ArbPort	0.32	3.05	ns	0.27	2.63	ns
	nbcav20	0.26	2.42	ns	0.2	1.98	ns
	openness	0.41	3.9	**	0.33	3.21	ns
	nbmh20	0.29	2.72	ns	0.24	2.35	ns
	nbmh56	0.3	2.84	ns	0.27	2.62	ns
	divmh20	0.29	2.5	ns	0.29	2.81	ns
	divmh56	0.31	2.67	ns	0.19	1.84	ns
	nbtree.7020m	0.23	2.13	ns	0.21	2.05	ns
	nbtree.7056m	0.32	3.04	ns	0.21	2.06	ns
Solitary	BMT	0.41	2.93	ns	0.38	3.32	ns
	DBH_ArbPort	0.59	4.23	**	0.47	4.06	ns
	NbMH_ArbPort	0.58	4.18	**	0.59	5.1	**
	DivMH_ArbPort	0.54	3.9	*	0.61	5.27	**
	nbcav20	0.5	3.6	*	0.42	3.63	ns
	openness	0.32	2.33	ns	0.29	2.54	ns
	nbmh20	0.45	3.25	ns	0.44	3.84	ns
	nbmh56	0.41	3.46	ns	0.53	4.58	*
	divmh20	0.48	2.96	*	0.55	4.75	*
	divmh56	0.41	2.96	ns	0.61	5.27	*
	nbtree.7020m	0.38	2.72	ns	0.38	3.33	ns
	nbtree.7056m	0.4	2.85	ns	0.38	3.31	ns

Table 8: CAP analyses results. Environmental drivers of species assemblages.

Synthèse de l'article 4

Article	Problématiques	Résultats Habitat	Résultats coléoptères saproxyliques	Points discutés	Questions soulevées	Perspectives d'étude	Conclusions
4	Quelle est l'importance relative des arbres solitaires par rapport à la forêt pour la conservation des coléoptères saproxyliques? Les arbres solitaires sont-ils des structures clés pour la conservation des espèces saproxyliques? Quelles sont les caractéristiques des arbres qui influencent leur valeur écologique à l'égard des coléoptères saproxyliques?	Variables plus importantes hors forêt: Ouverture de la canopée; quantité et diversité de dendromicrohabitats sur les arbres porteurs des pièges (ApP); nombre et diversité de dendromicrohabitats sur gros arbres (DBH>70cm) 20m autour du piège; cavités sur gros arbres 20m autour du piège. Variables plus importantes en forêt: Volume de bois mort; nombre de gros arbres. Aucune diférence: quantité de dendromicrohabitats sur les gros arbres à l'hectare; nombre de gros arbres 20m autour du piège (incluant l'arbre porteur).	Variation richesse spécifique: Aucune. Variation abondance: Aucune. Déterminants richesse spécifique: *Foret: Toutes espèces*: Aucun. *Espèces rares*: Diversité dendromicrohabitats à l'hectare (seuil à 2 dendromicrohabitats). *Arbres solitaires: Toutes espèces:* DBH ApP; Quantité et diversité dendromicrohabitats ApP (seuils respectifs 4 et 3). *Espèces rares*: Quantité et diversité dendromicrohabitats ApP (seuils respectivement 4 et 3); diversité des dendromicrohabitats à l'hectare (seuil à 3). Déterminants abondance: *Foret: Toutes espèces*: DBH ApP; Nombre de cavités sur gros arbres sur 0.3ha. *Espèces rares*: Aucun. *Arbres solitaires: Toutes espèces*: Quantité et diversité dendromicrohabitats ApP (seuils respectivement 3 et 2); diversité dendromicrohabitats à l'hectare. *Espèces rares*: Diversité dendromicrohabitats ApP (seuil à 1); ouverture du milieu. Assemblages d'espèces: *Toutes espèces:* différents à 47% entre forêt et arbres isolés. *Espèces rares*: différents à 62% entre forêt et arbres isolés. Dans les deux cas, 90% de la dissimilarité est expliquée par un turnover d'espèces. Espèces indicatrices*: Foret: espèces communes*: 39 espèces. *Espèces rares*: 3 espèces. *Arbres solitaires: Espèces communes*: 36 espèces. *Espèces rares*: 3 espèces. Determinant des assemblages: *Forêt: Toutes espèces*: Ouverture du milieu (3.9%). *Espèces rares*: Aucun. *Arbres solitaires: Toutes espèces*: DBH ApP (4.23%); quantité et diversité dendromicrohabitats ApP (respectivement 4.18 et 3.9%; Nombre de cavités à 0.3ha; diversité de dendromicrohabitats sur abres de DBH>70cm à 0.3ha. *Espèces rares*: Quantité et diversité de dendromicrohabitats ApP (respectivement 5.1 et 5.27%).	Habitat: Différences structurelles entre arbres isolés et arbres forestiers. Arbres isolés comme habitat en raréfaction. Espèces: espèces spécialistes des deux milieux étudiés. Déterminants de la richesse spécifique et de l'abondance différents entre forêt et arbres solitaires.	Prendre exemple sur les arbres solitaires pour améliorer la considération des arbres habitats en forêt? Quel devenir pour les arbres isolés et quid de la conservation des espèces qu'ils abritent?	Rétention d'arbres lors de l'exploitation finale du peuplement. Lesquels, combien, comment? Influence de la structure passée du paysage sur les assemblages actuels? Rôle effectif de 'stepping stones' des arbres isolés?	Forts enjeux de conservation de la faune des coléoptères saproxyliques associés aux arbres solitaires.

Tableau 6 : Are solitary trees keystone structures for saproxylic biodiversity conservation? Problématiques, résultats, éléments particuliers discutés, nouvelles problématiques posée, perspectives d'études à envisager et conclusions pricipales de l'article.

Chapitre IV :

Effets paysagers

Chapitre IV : Effets paysagers

Ce chapitre se structure en deux parties. Nous présentons en premier lieu une étude portant sur la quantité d'habitat dans le paysage et l'impact que cela a sur les assemblages locaux de coléoptères saproxyliques. En second lieu, nous présentons un projet de co-analyse franco-tchèque de l'évolution de la structure paysagère sur les assemblages de coléoptères saproxyliques.

Publications associées à ce chapitre : Articles **7**[2] et **8** (cf Tableau 2).

Partie I : Influence de la proportion de réserves dans le paysage sur les assemblages locaux de coléoptères saproxyliques.

Les relations entre les espèces et leur habitat existent à plusieurs échelles spatiales, en allant de l'échelle locale (effet de variables structurelles fines) à l'échelle paysage (influence de variables structurelles plus larges). Cette relation habitat / espèces à différentes échelles est également observée pour les espèces de coléoptères saproxyliques (Holland *et al.,* 2005 ; Bergman *et al.,* 2012).

L'habitat des coléoptères saproxyliques est actuellement fortement impacté par les activités forestières. Les mesures de conservation mises en place actuellement ne permettent de protéger qu'une très faible partie de la surface forestière. Ces parties soustraites à l'exploitation forestière représentent des zones à fort potentiel d'habitat pour les espèces saproxyliques. Elles sont cependant mal réparties spatialement au sein de la forêt, généralement en une seule tache. Il existe donc au sein des forêts une matrice restreinte d'habitat de très grande qualité (les réserves) entourée de zones d'habitat de moins bonne qualité (les zones exploitées). L'habitat des espèces saproxyliques s'en retrouve fortement fragmenté au sein de la forêt.

Nous avons montré dans le Chapitre III que la mise en réserve était efficace pour la reconstitution des volumes de bois mort et de la quantité de dendromicrohabitats, si la durée de mise en réserve est importante. L'effet ponctuel des réserves est également positif sur les coléoptères saproxyliques, mais son efficacité varie avec la durée de non-exploitation : plus la réserve est ancienne, plus les effets sont prononcés.

Mais quel est l'effet des réserves forestières sur les assemblages de coléoptères saproxyliques à l'échelle de la forêt ? Comment les zones exploitées sont-elles affectées par les réserves avoisinantes ?

Nous avons mené une investigation de l'effet paysager de la densité de réserves sur les assemblages de coléoptères saproxyliques contactés dans les zones exploitées voisines.

Nous avons mis en évidence des effets positifs de l'augmentation de la densité de réserves dans la matrice forestière du paysage à travers deux possibles effets distincts : (i) l'effet de spillover (Rowse *et al.,* 2011), et (ii) l'effet de masse (Fahrig, 2013). Nous avons mis en évidence l'existence de seuils de densités de réserves dans le paysage permettant la sauvegarde d'un nombre d'espèces accru.

[2] L'article 7 a été acceptéaprès modifications dans la revue Conservation biology. Un pdf des épreuves non corrigées est disponible en Annexe 4.

Article 7: Increasing the percentage of forest reserves in the landscape amplifies saproxylic beetle diversity both within and beyond reserve borders

G. Parmain*,°,**, C. Bouget*

* National Research Institute of Science and Technology for Environment and Agriculture. (IRSTEA), 'Forest ecosystems' Research Unit, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France (christophe.bouget@irstea.fr; guilhem.parmain@irstea.fr).

° National Laboratory of Forest Entomology, National Forest Office (ONF), F-11500 Quillan, France. (guillem.parmain@onf.fr)

** National Museum of Natural History, Natural Patrimony Department, 36 rue Geoffroy St Hilaire, CP 41 75 231 PARIS CEDEX 05, France.

Abstract:

Increasing the density of natural reserves in the forest landscape may provide conservation benefits for biodiversity in both surrounding unprotected habitats (spillover effect hypothesis) and in the reserves themselves (habitat amount effect hypothesis).

We tested both hypotheses using two French datasets on saproxylic beetles and landscape cover of forest reserves (LCFR) quantified at five nested landscape scales from 500m to 2500m around biodiversity assessment plots: (i) a national standardized dataset with 252 plots in both managed and unmanaged stands in nine lowland and five highland forests, and (ii) a detailed case study in the lowland Rambouillet forest, a forested landscape rich in reserves. Biodiversity conservation measures like reserves designed to create a functional network were pioneered in the Rambouillet forest. This forest was studied by the GNB and RESINE projects, with a denser sampling design in the latter, leading to a large entomological dataset.

A positive influence of LCFR on saproxylic diversity in adjacent harvested stands (spillover effect) was demonstrated, more strongly in highland than in lowland forests, and in the Rambouillet area than in other lowland sites, probably due to contrasts in reserve quality. Most LCFR thresholds among the significant relationships were about 20%, a pivotal landscape proportion of suitable habitat advanced in previous studies. In lowland but not in highland forests, the LCFR also affected species richness in the reserves themselves (habitat amount effect). In the Rambouillet forest, an increasing number of reserve patches fostered the abundance of rare species in reserves.

We show how increasing reserve density enhances biodiversity conservation both within and beyond reserve borders. Habitat cover thresholds could help managers to define targets for nature conservation.

Key-words: Threshold, forest management, temperate forest, habitat amount, rare species, spillover effect, SLOSS.

Abbreviation: LCFR= Landscape Cover of Forest Reserves

Introduction:

Global efforts to slow biodiversity loss include improving natural reserve designs, but the amount of protected habitat in managed territories remains restricted due to human land use. Reserves would be more efficient if their conservation benefits extended beyond their boundaries into surrounding unprotected habitat—a process called "spillover" (Gell and Roberts, 2003). The spillover effect is characterized by three elementary processes: the refuge effect (forest reserves are more suitable habitats), environmental stability (fewer disturbances due to lack of harvesting) and a high number of individuals dispersing outside the forest reserve (Brudvig *et al.,* 2009; Russ and Alcala, 2011). The spillover effect is conceptually close to the spatial mass effect (or vicinism; Shmida and Ellner, 1984), which assumes that a species can occur in an unfavourable habitat, despite low reproductive success and fitness, thanks to the influx of propagules from a source population living in a nearby favourable habitat (Shmida and Ellner, 1984). The initial model for spillover was developed at the population level. Due to its heuristic value in conservation ecology, the model has been extended from single species to species communities: spillover should cause species enrichment around reserves that host large numbers of species.

Due to the generalized forestry-induced depletion of their substrates in managed forests worldwide, deadwood-associated, i.e. saproxylic, species' biodiversity is at stake. Forest reserves are known to harbour higher densities of old-growth structures such as old trees and dead wood, favourable to saproxylic organisms, than does the harvested forest matrix (Bouget *et al.,* 2014). As a result of within-patch dynamics, reserves may be thought to support an increased density of saproxylic beetle species, leading to a spillover of these species into the surrounding stands where deadwood substrates have been reduced by forestry. We assume that in highland forests, reserves have often been established in less accessible sites difficult and expensive to harvest than in lowland forests. As a consequence, spillover and mass effects may produce different effects in lowland or highland stands.

In fine-grain, managed forests in Western Europe, forest reserve patches are often small and scattered in the landscape, reducing local saproxylic population sizes and impeding their dispersal (Tscharntke *et al.,* 2002). A spillover effect can be detected by checking for biodiversity variations along two gradients of habitat isolation: i) the distance to neighbouring reserves, or ii) the proportion of reserves within the forest landscape, hereafter called Landscape Cover of Forest Reserves (LCFR). The distance to the nearest neighbouring habitat patch has proven to be a less predictive variable than buffer zone indicators (Moilanen and Nieminen, 2002). The literature in forest ecology provides more evidence of a significant positive effect of neighbouring old-growth stands on biodiversity in terms of surrounding density (Abrahamsson *et al.,* 2009; Edman *et al.,* 2004; Franc *et al.,* 2007; Olsson *et al.,* 2012) rather than in terms of linear distance (McGeoch *et al.,* 2007). We hypothesized

that higher LCFR would lead to stronger spillover effects and, consequently, to increased species richness or abundance in surrounding areas traditionally managed for harvesting.

The density of reserves in the landscape may also affect the species richness in the reserves themselves. Indeed, the "habitat amount hypothesis" predicts that species richness in equal-sized sample sites in reserve areas should increase with the total amount of reserve habitat in the 'local landscape' surrounding the sample site, the local landscape being the area within an appropriate distance of the sample site (Fahrig, 2013).

In addition to the question about reserve proportion effects at the forest and landscape levels on species diversity, the spatial organisation of reserves is debated. The same amount of forest reserve can be used within two ways: Single One or Several Small reserve patches. Each strategy had practical advantages and inconvenient for the forest manager. For biodiversity conservation, both strategies seemed to be useful, but depended on the context to be applied (Tjørve, 2010) this seemed particularly true for forests (Ranius and Kindvall, 2006).

We analysed saproxylic beetle data from fourteen French temperate forests to address the following five questions. 1) In accordance with the spillover hypothesis, is reserve cover in the surrounding forest landscape a significant factor in predicting variations in local species richness on harvested plots? 2) In line with the habitat amount hypothesis, does reserve cover in the surrounding landscape significantly affect the local species richness in the reserves themselves? 3) Is the situation the same in lowland and in highland forests? 4) Are all species affected or are only rare species concerned (possibly more sensitive to the distribution pattern of reserves)? 5) At the Rambouillet forest case study scale, does the number of reserve patches affect local species richness after accounting for the effects of reserve cover?

Material and methods

Study sites

Two hundred and fifty two plots - 111 plots in forest reserves and 141 in managed stands - were set up in 14 French forests (9 lowland and 5 highland forests) (Tab. 1). All study forests included both managed and unmanaged plots. The study plots were selected in adult stands (at least 100 years old). The dominant tree species varied, from spruce with fir and beech to beech with oak and hornbeam (see Tab. 1). Among our study sites, the Rambouillet forest is a special case. Certain biodiversity conservation measures were pioneered in this 22,000-ha state oak forest in northern France, 50 km west of Paris, which currently includes a high number of forest reserves that have remained unmanaged for more than 80 years. These reserves were designed to create a functional network for biodiversity conservation. The Rambouillet forest was studied by the GNB and RESINE projects, with a denser sampling design in the latter.

Beetle data

Flying saproxylic beetles were sampled with two unbaited cross-vane flight interception traps (PolytrapTM, E.I. Purpan, Toulouse, France) per plot, set about 20 m from each other, except for the "Bois du Parc" and "Haut-Tuileau" sites where only one trap per plot was set. A total of 478 traps was set. The traps were suspended roughly 1.5 m above the ground. Active insects were collected from

April to August (see Tab. 1 for further details on sampling years). For each species in all the taxa identified from the ±50 families recorded, we characterized the degree of geographic rarity in France according to the FRISBEE database (http://frisbee.nogent.cemagref.fr/index.php/en/) and distinguished rare species (not abundant and only locally distributed) from the others. The resolution of species identification was higher for the detailed RESINE dataset than for the 14 GNB standardized datasets. In the standardized low-resolution beetle dataset, we only considered the families systematically identified at all sites (though we did also include easily-identifiable rare families such as Cerophytidae or Nosodendridae present in only one or two forests). In addition, the high-resolution RESINE dataset was considered separately, with a dedicated objective (see below). We computed three response variables for each trap: total species richness (Rstot), rare species richness (Rsrar) and rare species abundance (Abrar).

Landscape and environmental data

While studying landscape effects on oak saproxylic beetles from the local (52m) to the large scale (5200m), Bergmann et al. (2012) found the 2300m scale to be outstanding. Herein the present study, we used a GIS system (ArcGis 10.2) to quantify the proportion of forest area set aside as natural forest reserves (LCFR), at five nested spatial scales (500m, 1000m, 1500m, 2000m, 2500m) around each plot (buffer zones). When few patches of forest reserve were available on our study sites, the Rambouillet forest possess more than 20 of such reserve patches. We computed the number of forest reserve patches inside each buffer In the Rambouillet forest only. The dead wood volume on each plot was already available (see Bouget *et al.,* 2014, for further details on dead wood volume estimations).

Data analysis

Two datasets were available for analysis: (i) a nationally compiled, standardized dataset with lower taxonomic resolution for beetles, but with a larger overall sample size, a broader landscape coverage including both lowland and highland forests, and more regional replicates; and (ii) a detailed case study (RESINE) of the lowland Rambouillet forest offering high-resolution beetle data, and more numerous, though more locally specific, reserves in the forest mosaic landscape (fewer replicates, a single lowland forest area).

On the national dataset, we performed separate analyses for lowland and mountain sites due to differences in the mean specific richness per trap and potential divergences in average management history. To account for between-trap differences due to local within plot contrasts in resource availability, we included the local deadwood volume as a primary covariate in the analytical models. Depending on the distribution pattern of response variables (total species richness, abundance and richness of rare species), we used linear (lmer) or generalized linear (glmer, family=Poisson) mixed models. *Forest* was used as a random factor in all mixed models. An observation-level random effect was added in the generalized linear mixed models to account for data over-dispersion. The effects of LCFR on beetle response variables were assessed at each of the five nested spatial scales, in harvested and in reserve stands, using a likelihood ratio test between the models with and without the predictor. The best spatial scale, at which the highest explanatory power was measured, was identified by model comparisons of AICc values for each response variable, in both harvested and in reserve stands.

For the specific RESINE case study, we performed a Pearson's correlation test between the number of reserve patches and LCFR at the five landscape scales. The two predictors were strongly correlated at the 500m and 1000m spatial scales but not at the 1500m, 2000m and 2500m scales. We used glmer models with LCFR and the number of reserve patches as additive effects at the 1500m, 2000m and 2500m scales only, including deadwood volume as a primary covariate. The significance of ecological effects was assessed by model comparisons using likelihood ratio tests.

We used recursive partitioning (Hothorn and Zeileis, 2008) to search for thresholds in the significant models. This approach makes it possible to simultaneously identify a threshold and assess its significance by means of a statistical test procedure. The thresholds are derived from estimates of breakpoints revealed in maximally selected two-sample statistics. Their validity is judged by multiple test procedures. This method provides a decision tree with p-values for one or more critical thresholds. Based on 1000 bootstrap samples, a confidence interval (IC; 95%) was calculated for all thresholds. The significant p-value for thresholds was set at $p<0.01$. Each of the two groups separated by a threshold had to contain at least eight samples to be selected.

All analyses were carried out with the R 3.1.0 (R Core Team, 2013) software.

Results

Overall, the compiled standardized dataset included 460 species and 179,237 individuals, whereas the detailed RESINE dataset had 335 species and 137,154 individuals.

In the following threshold type relations between species richness or abundance and environmental variables, the slope of the species (or individual) accumulation rate was always steeper beyond the detected threshold point.

1. Beetle diversity response to LCFR in harvested plots (spillover hypothesis)

Highland forests (national dataset). In managed highland stands, the total species richness increased with LCFR at the 2500m scale; no threshold could be identified for this slightly significant relationship (Fig. 1a). The LCFR also significantly contributed to local variations in rare species richness and abundance. Indeed, the number of rare species increased with LCFR, markedly so beyond the threshold value of 36.5% (IC: 0.0-38.6) of forest reserves in the 500m-radius landscape buffer (Fig. 1b). Similarly, the abundance of rare species was positively affected by an increasing LCFR and a threshold value of 21.5% (IC: 9.2-24.8) of forest reserves in the 1500m landscape (Fig. 1c) was detected in the relationship.

Lowland forests (national dataset). Neither overall assemblage richness nor rare species abundance or richness significantly responded to variations in LCFR in lowland managed stands.

Lowland forests (RESINE case study). In managed plots in the Rambouillet forest case study, the relationship between beetle diversity and LCFR was not significant. However, after taking LCFR into account, an increase in the number of reserve patches positively affected the local number of species in managed stands at the 2500m landscape scale. The overall species richness of saproxylic beetle assemblages was amplified beyond the threshold value of two reserve patches in the 2500m-radius landscape buffer (IC: 1-3; Fig. 1d).

2. Beetle diversity response to LCFR in reserve plots (habitat amount hypothesis)

The saproxylic beetle species response to LCFR was contrasted in unmanaged stands.

Highland forests (national dataset). No response of saproxylic beetle diversity to LCFR was observed in highland unmanaged stands. No significant trends were detected for the response of rare species to LCFR in unmanaged stands.

Lowland forests (national dataset). A significant, positive relationship was identified between LCFR in a 500m-radius landscape buffer and the total species richness in lowland forests (Fig. 2a), though no threshold value was apparent.

Lowland forests (RESINE case study). An increase in LCFR enhanced the local richness of all species in unmanaged plots at the 2500m landscape scale. This effect was even stronger beyond a threshold value of 20.0% (IC: 20.0-20.9) of LCFR (Fig. 2b). The number of reserve patches in the 2500m-radius landscape buffer also significantly affected the abundance of rare species, though no threshold value was detected in this relationship (Fig. 2c). The number of reserve patches had no significant effect on total or rare species richness in unmanaged plots.

3. Comparison of biodiversity responses at the five nested spatial scales

Overall, we observed significant relationships between LCFR and species richness or abundance for rare saproxylic beetle species and all species combined at all the five spatial scales from 500m to 2500m (Tab. 2). In lowland forests, all the best models (i.e. with the lowest AICc) occurred at the 500m scale, whatever the response variable, whereas they always related to larger scales in highland forests. All the best models identified in the Rambouillet case study related to the large 2500m spatial scale.

Discussion

1. Effects of the density of reserves on local assemblages in managed areas: spillover effects?

Our sampling scheme was not especially designed to demonstrate spillover effect. In consequence, we were not able to directly demonstrate spillover from protected to unprotected areas. However, we did demonstrate that landscape reserve design can benefit biodiversity beyond reserve borders, possibly by promoting spillover. The positive influence of LCFR on biodiversity in adjacent managed stands was observed in both lowland and in highland forests.

The possible spillover effects we observed in harvested areas seemed more efficient in highland than in lowland contexts. Among lowland sites, a greater effect was measured in the Rambouillet forest than in other lowland sites. These results may be related to the higher ecological quality of the reserves compared to the harvested areas. In highland forests, reserves have often been established in less accessible sites, mainly characterized by steep slopes, and which are technically difficult and expensive to harvest. Due to their topographical constraints, these sites have been abandoned for a

long time, or they have a limited harvesting history. In contrast with harvested areas, they may host a higher density of old-growth legacies. In lowland forests, site selection for reserves usually attempts to limit future losses of income from lack of harvesting. Reserves are therefore established on sites with little silvicultural interest, even if their conservation interest may also be low. The Rambouillet forest is a special case among lowland sites since reserves there have mainly been established based on their conservation interest, i.e. on sites with high substrate continuity in the past.

Spillover effects were initially studied in marine ecosystems (McClanahan and Kaunda-Arara, 1995), and have only recently been documented in terrestrial ecosystems: for insects from natural habitats to crop plantations (Hanley *et al.,* 2011; Lucey and Hill, 2012) and for plants (Brudvig *et al.,* 2009). Forest reserves may act as nurseries for saproxylic beetle species thanks to their higher-quality habitat compared to the surrounding harvested forest matrix (Bouget *et al.,* 2014). In reserve areas, an increase in population levels may enable more dispersers to emigrate to nearby harvested stands. Landscape effects on the survival probability of individual species - and consequently on the local number of species persisting in matrix habitats - may be related to metapopulation processes, with recolonizing events counterbalancing local extinctions in fragmented landscapes (Hanski and Gaggiotti, 2004). Having more reserves inside a landscape buffer also improves connectivity and facilitates exchanges of individuals and species among reserve patches, thereby causing a connectivity-enhanced spillover effect (Brudvig *et al.,* 2009).

The importance of the surrounding landscape for local species richness, here attested in highly fragmented temperate forests in Western Europe, is in line with suggestions by Lassauce *et al,* (2011) and Bouget *et al,* (2013), who both demonstrated that local saproxylic biodiversity is not strongly driven by the quantity of locally available deadwood substrates. From Janssen *et al,* (2009), even in boreal contexts, the combined influence of structural and compositional habitat heterogeneity at stand and landscape scales best explains richness patterns in flying saproxylic beetles.

Among the five nested landscape scales we studied, we did not identify a univocal scale for the effects of forest reserve cover on biodiversity, whatever the altitudinal context or the response variable. Potential spillover effects were detected at all scales, from 500m to 2500m. Large scale (Bergmann *et al.,* 2012; Franc *et al.,* 2007) and small scale (Schiegg, 2000) landscape effects on local saproxylic beetle species richness have already been found. From Holland *et al,* (2004), the great disparity in species dispersal ability among saproxylic beetles impedes the detection of a single connectivity scale for the whole species assemblage.

2. Effects of the density of reserves on local assemblages in reserves: habitat amount effects

The LCFR significantly affected species richness in the reserves themselves in lowland but not in highland forests. The LCFR fostered species richness in reserves at the 500m scale in the compiled dataset of nine lowland forests, and at the 2500m scale in the Rambouillet case study. In the latter case, the number of reserve patches also fostered the abundance of rare species in reserves. These positive influences of the LCFR are in line with the habitat amount hypothesis (Fahrig, 2013). Our test of the habitat amount hypothesis relies on a habitat/non-habitat view of the landscape, even though it is difficult to ecologically delineate reserves as discrete habitat patches for a species group. It should be borne in mind that saproxylic habitats (e.g. old-growth structures) that exist in reserve patches also occur in the surrounding landscape, though at a lower density or with less continuity in

time. Saproxylic habitats in the managed matrix may be at least partly habitable for some of the species living predominately in reserves, with reduced breeding success or fitness in them.

3. Response thresholds to the proportion of reserves in the surrounding forest area

Habitat thresholds may help managers to define targets for nature conservation (Müller and Bütler, 2010). We showed the importance of non-linear relationships between landscape patterns and biodiversity. We identified thresholds in some of the significant relationships between LCFR and total species richness or rare species richness. In all cases, the species accumulation rate strongly increased beyond the threshold value, i.e. the local extinction probability of species decreased. These thresholds correspond to the amount of habitat below which fragmentation may affect population persistence (Andrén, 1994). Even though confidence intervals were wide, and could probably be improved with larger datasets, most of the significant threshold values we detected were at about 20% of suitable habitat, i.e. forest reserve cover, in the surrounding landscape. Several authors have already suggested conserving 20–30 % of favourable habitats for biodiversity conservation at the landscape scale. Using a simulation approach, Andrén (1994) found that the regional extinction rate of vertebrates increased when favourable habitat fell below a threshold of 20 to 30%. Nilsson *et al,* (2001) recommended conserving 20 % of the original density of habitat at the landscape scale to preserve biodiversity. Similar values were also recommended by Wiktander *et al,* (2001) for the lesser spotted woodpecker (*Dendrocopos minor*) and by Wegge and Rolstad (1986) for the Capercaillie (*Tetrao urogallus*). Empirical studies on saproxylic longhorn beetles pointed out that extinction thresholds differ widely among species (Holland *et al.,* 2005). From Ranius and Jonsson (2007), distinct thresholds in habitat availability at the species assemblage level would be difficult to determine (Ranius and Fahrig, 2006). Nevertheless, high values of landscape reserve cover are likely to encompass most saproxylic species' habitat requirements.

It should be remembered that a global target of 17% of the forested land area as reserves was set at the UN biodiversity summit in Nagoya in 2010 (Hanski, 2011). A target of 20% of reserves in forest landscapes is nonetheless very ambitious compared to the current proportion of forest reserves across Europe: 7.6% on average (Parviainen *et al.,* 2000) ranging from 1.2% of the total forest cover in France to 24.0% in Spain. Only Spain, Denmark and Hungary have a proportion of protected forests which slightly exceeds the 20% threshold. From 2000 to 2011, efforts in French public forests have raised the surface area from 1.2% to 6.7% of the forested landscape (ONF, 2011). Fortunately, a large proportion of the private forests in France, with their fragmented ownership, has been left unmanaged and unharvested; these patches act as unofficial passive reserves.

4. Reserve design and the SLOSS insights

Our results from the RESINE case study in Rambouillet provide important information about the spatial design of reserves. In the managed forest matrix, with the reserve surface area being accounted for, the higher the number of surrounding reserve patches, the higher the reserve effect on local species richness, and therefore the stronger the spillover effect. In other words, at the 2500m scale, several small reserves more efficiently increased beetle species richness outside the reserves than did one single large reserve. In the reserves themselves, the number of patches did not

change the reserve effect on local species richness. Nonetheless, rare species abundance inside reserves was strongly improved by increasing the number of reserve patches.

The spatial configuration of forest reserves in the landscape is a recurrent issue in biodiversity conservation (Groom *et al.,* 2006). For instance, the SLOSS debate (Single Large Or Several Small) questions whether managers should split conservation efforts (total reserve surface area) into several units or instead set up one large unit. Results from field data are contrasted, underlining the need for individual case studies to determine the best local strategy (Tjørve, 2010). Using metapopulation models, Ranius and Kindvall (2006) founded different optimal reserve spatial configuration depending on forest harvesting history. In unharvested forest, models predicted few number of large forest reserve to be more efficient than many small. In contrary, in harvested forests, many small forest reserves were more efficient than several large. In harvested forests, small plots with high habitat quality could be selected, when large reserves contained habitats both of high and low quality (Ranius and Kindvall, 2006). Some studies provide guidelines for the minimum size of unharvested patches required to host a maximum diversity of substrates: at least 20 ha for tree microhabitats (Larrieu *et al.,* 2014), at least 2 ha for deadwood types (Jakoby *et al.,* 2010). Ovaskainen (2002) suggested that several large patches of habitat maximize species metapopulation capacity. This is in line with our findings: several large forest reserve patches in the landscape seemed to be more valuable for strengthening forest species metapopulations, e.g. saproxylic beetle populations, than one single reserve patch.

In the present article, we provide data on the effects of the size and number of forest reserves on biodiversity. Nevertheless, it should be borne in mind that (i) other criteria, such as patch shape, edge length and contrast, connectivity and corridors also determine reserve conservation value; and that (ii) selection criteria in any forest conservation strategy should consider not only conservation value but also management costs. Large ecological reserves may be easier to protect from an organizational perspective. Conversely, single, large ecological reserve units are rarely comprehensive in terms of habitats, nor are they representative of all elements of biodiversity.

Forest managers may therefore be better off protecting a wider range of habitats through smaller reserve patches distributed throughout the fine-scale mosaic of European habitat types, or at least to adopt multi-scaled conservation measures.

In our study, we limited our investigation to total species richness and to rare species richness and abundance. It should however be kept in mind that not all species depend on reserve patterns equally (Tscharntke *et al.,* 2002). For example, specialist species depending on habitats that exist mainly in reserve patches may be more affected by reserve patterns than generalists, since the surrounding landscape is at least partly inhabitable for generalists. Good dispersers may be less affected by reserve patterns than little mobile species, which are not able to disperse between isolated patches in a loose reserve network. We therefore suggest that reserve patches could also provide interesting study areas for individual species abundance and occurrence.

Conclusions

We show how increasing reserve density enhances biodiversity both within and beyond reserve borders. Further research is required to define relevant management guidelines for reserve system design in order to increase levels of biodiversity spillover, in particular in relation to the two reserve properties most often taken into account, patch connectivity and patch shape. Our threshold values may provide forest reserve cover percentage targets, even though they may be difficult to reach in managed European landscapes. Establishing reserves in valuable habitat patches, which have not been severely degraded by intensive forestry practices, is of primary concern. Indeed, the colonization by saproxylic beetles is a very slow process which requires an even longer time frame than does habitat restoration (Bouget *et al.,* 2014).

Aknowledgements

We are grateful to C. Moliard, B. Nusillard, Y. Paillet, F. Gosselin (Irstea), T. Barnouin, F. Soldati, T. Noblecourt (ONF), N. Debaive (RNF), J.L. Témoin, M. Bonafonte (ONF Rambouillet) and all the local forest managers for their field and laboratory work and assistance. We are also indebted to Vicki Moore who reviewed the English manuscript. This research was granted by the French ministry in charge of the Ecology through the "Biodiversité, Gestion Forestière et Politiques Publiques" (BGF) program (RESINE CVOJ 000 150 convention, 10-MBGD-BGF-1-CVS-092 convention, n°CHORUS 2100 214 651) and the National Forestry Board ("Office National des Forets", ONF-Cemagref convention, Action 5, 2008).

References

Abrahamsson, M., Jonsell, M., Niklasson, M., Lindblahd, M., 2009. Saproxylic beetle assemblages in artificially created high-stumps of spruce (Picea abies) and birch (Betula pendula⁄pubescens) – does the surrounding landscape matter? *Insect Conservation and Diversity* **2**, 284–294.

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**; 355-366.

Bergman, K.O., Jansson, N., Claesson, K., Palmer, M.W., Milberg, P., 2012. How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. *Forest Ecology and Management* **265**, 133–141.

Bouget, C., Larrieu, L., Parmain, G., Nusillard, B., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation* **22**, 2111–2130.

Bouget, C., Parmain, G., Gilg, O., Noblecourt, T., Nusillard, B., Paillet, Y., Pernot, C., Larrieu, L., Gosselin, F., 2014. Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? *Animal Conservation* doi:10.1111/acv.12101.

Brudvig, L.A., Damschen, E.I., Tewksbury, J.J., Haddad, N.M., Levey, D.J., 2009. Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 9328-9332.

Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B., Ericson, L., 2004. Spore deposition of wood-decaying fungi: importance of landscape composition. *Ecography* **27**, 103-111.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* **40**, 1649–1663.

Franc, N., Gotmark, F., Okland, B., Norden, B., Paltto H., 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biological Conservation* **135**, 86-98.

Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: The fishery effect of marine reserves. *Trends in Ecology and Evolution* **18**, 448–455.

Groom, M.J., Meffe, G.K., Carroll. C.R., 2006. *Principles of conservation biology*, Sinauer, 3rd edition.

Hanley, M.E., Franco, M., Dean, C.E., Franklin, E.L., Harris, H.R., Haynes, A.G., Rapson, S.R., Rowse, G., Thomas, K.C., Waterhouse, B.R., Knight, M.E., 2011. Increased bumblebee abundance along the margins of a mass flowering crop: evidence for pollinator spill-over. *Oikos* **120**, 1618–1624.

Hanski, I., 2011. Habitat Loss, the Dynamics of Biodiversity, and a Perspective on Conservation. *Ambio* **40**, 248-255.

Hanski, I., Gagiotti, O.E., (Eds) 2004. *Genetics and evolution of metapopulations*. Academic press, 696p.

Holland, J.D., Bert, D.G., Fahrig, L., 2004. Determining the Spatial scale of species responses to habitat. *BioScience* **54**, 227-233.

Holland, J.D., Fahrig, L., Cappuccino, N., 2005. Body size affects the spatial scale of habitat/beetle interactions. *Oikos* **110**, 101-108.

Hothorn, T., Zeileis, A., 2008. Generalized maximally selected statistics. *Biometrics* **64**, 1263-1269.

Jakoby, O., Redemacher, C., Grimm, V., 2010. Modelling dead wood islands in European beech forests: how much and how reliably would they provide dead wood? *European Journal of Forest Research* **129**, 659-668.

Janssen, P., Fortin, D., Hébert, C., 2009. Beetle diversity in a matrix of old-growth boreal forest: Influence of habitat heterogeneity at multiple scales. *Ecography* **32**, 423-432.

Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., Deconchat, M., 2014. Tree microhabitats at the stand scale in montane beech-fir forests: practical information for taxa conservation in forestry. *European Journal of Forest Research* **133**, 355-367.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: Meta analyses of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators* **11**, 1027-1039.

Lucey, J.M., Hill, J.K., 2012. Spillover of Insects from Rain Forest into Adjacent Oil Palm Plantations. *Biotropica* **44**, 368-377.

McClanahan, T.R., Kaunda-Arara, B., 1995. Fishery Recovery in a Coral-reef Marine Park and Its Effect on the Adjacent Fishery. *Conservation Biology* **10**, 1187-1199.

McGeoch, M., Schroeder, M., Ekbom, B., Larsson, S., 2007. Saproxylic beetle diversity in a managed boreal forest: importance of stands characteristics and forestry conservation measures. *Diversity and Distributions* **13**, 418-429.

Moilanen, A.,Nieminen, M., 2002. Simple connectivity measures in spatial ecology. *Ecology* **83**:1131–1145.

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research* **129**, 981–992.

Nilsson, S.G., Hedin, J., Niklasson, M., 2001. Biodiversity and its Assessment in Boreal and Nemoral Forests. Scandinavian. *Journal of Forest Research (Suppl)* **3**, 10-26.

Olsson, J., Johansson, T., Jonsson, B.G., Hjalten, J., Edman, M., Ericson, L., 2012. Landscape and substrate properties affect species richness and community composition of saproxylic beetles. *Forest Ecology and Management* **286**, 108-120.

ONF, 2011. *Bilan patrimonial des Forêts Domaniales hors DOM*. ONF Paris, 180 pp.

Ovaskainen, O., 2002. Long-Term Persistence of Species and the SLOSS Problem. *Journal of Thoretical Biology* **218**, 419–433.

Parviainen, J., Kassiounis, K., Bücking, W., Hochbichler, E., Päivinen, R., Little, D., 2000. *Forest reserves research network in Europe.* The Finnish Forest Research Institute, Joensuu Research Station, 28p.

R Core Team., 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ranius, T., Fahrig, L., 2006. Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. *Scandinavian Journal of Forest Research* **21**, 201-208.

Ranius, T., Jonsson, M., 2007. Theoretical expectations for thresholds in the relationship between number of wood-living species and amount of coarse woody debris: A study case in spruce forests. *Journal for Nature Conservation* **15**, 120-130.

Ranius, T., Kindvall, O., 2006. Extinction risk of wood-living model species in forest landscapes as related to forest history and conservation strategy. *Landscape Ecology* **21**, 687-698.

Russ, G.R., Alcala, A.C., 2011. Enhanced biodiversity beyond marine reserve boundaries: the cup spillith over. *Ecological Applications* **21**, 241-250.

Schiegg, K., 2000. Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience* **7**, 290-298.

Shmida, A., Ellner, S., 1984. Coexistence of plant species with similar niches. *Vegetatio* **58**, 29–55.

Tjørve, E., 2010. How to resolve the SLOSS debate: Lessons from species-diversity models. *Journal of Theoretical Biology* **264**, 604-612.

Tscharntke, T., Steffan-Dewenter I., Kruess A. and Thies C. 2002. Characteristics of insect populations on habitat fragments: a mini review. *Ecological Research* **17**: 229–239

Wegge, P., Rolstand, J., 1986. Size and spacing of capercaillie leks in relation to social behavior and habitat. *Behavioural and Ecological Sociobiology* **19**, 401-408.

Wiktander, U., Olsson, O., Nilsson, S., 2001. Seasonal variation in home range size, and habitat area requirement of the lesser spotted wood pecker Dendrocopos minor. *Biological Conservation* **100**, 387-395.

Figures

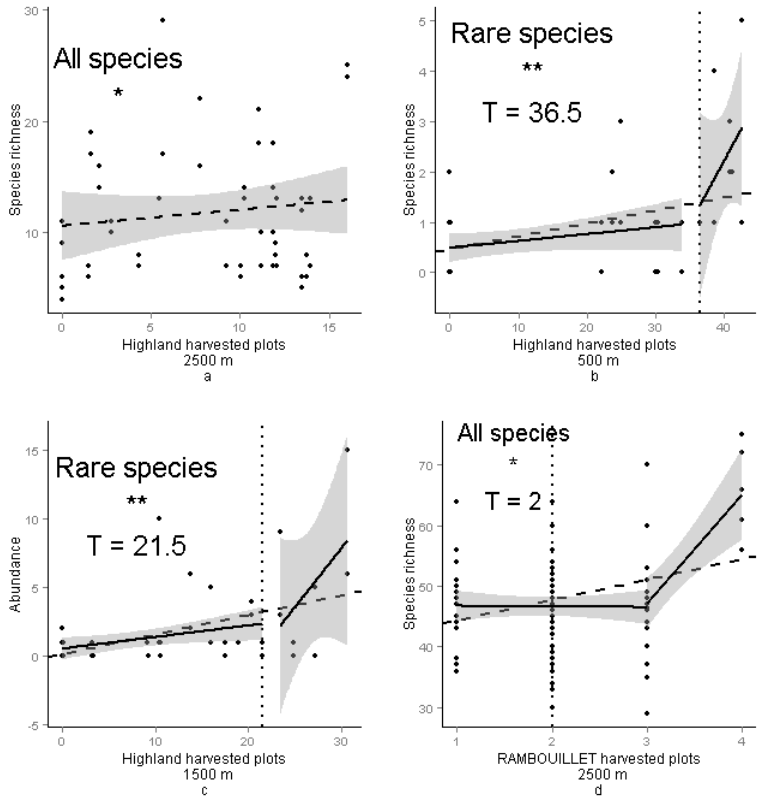


Figure1: Response of beetle diversity in harvested plots to the landscape cover of forest reserves in highland forests (no significant responses were actually observed in lowland forests) and patches number in the Rambouillet forest case study (spillover hypothesis). Reserve proportion in the forest landscape on X axes for **a**;**b** and **c** figures. Patches number on X axes for figure **d**. **a:** Total species richness at the 2500 scale; **b:** Rare species richness at the 500m scale; **c:** Abundance of rare species at the 1500m scale (mean values per trap); **d:** Total species richness in managed plots at the 2500m scale in the Rambouillet forest case study. Dashed line: linear species accumulation rate. Continuous line: species accumulation rate before and after threshold (vertical line, T = threshold). Grey areas are standard deviations of accumulation rate curves. They are represented on global species accumulation rate when no threshold appears, and on species accumulation rate before and after threshold lines when a threshold occurs.

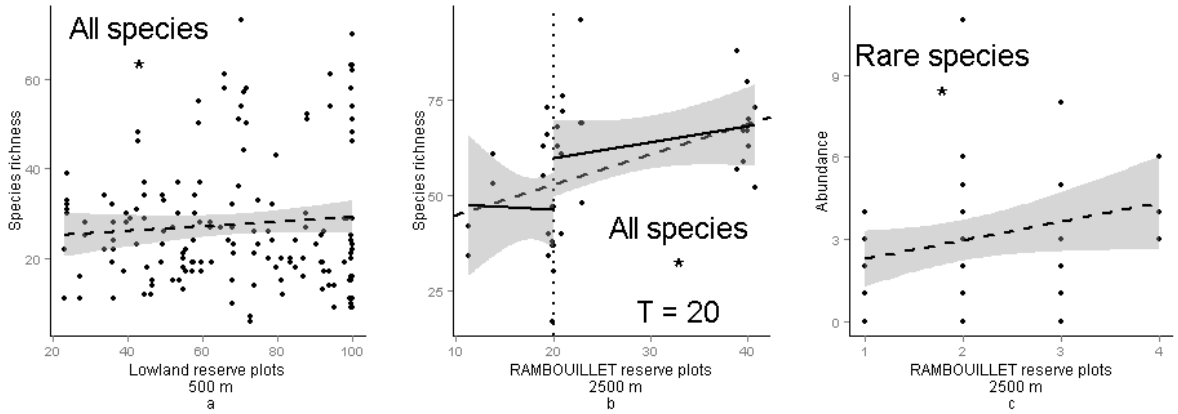


Figure 2 Response of beetle diversity in reserve plots to the landscape cover of forest reserves in lowland forests (no significant responses were actually observed in highland forests) and in the Rambouillet forest case study (habitat amount hypothesis). Reserve proportion in the forest landscape on X axes for figures **a** and **b**. Patches number on X axes for figure **c**. **a:** Total species richness at the 500m scale in lowland forests (pooled data from 9 forests); **b:** Total species richness at the 2500m scale in the Rambouillet forest case study; **c:** Abundance of rare species in reserve plots at the 2500m scale in the Rambouillet forest case study. Dashed line: linear species accumulation rate. Continuous line: species accumulation rate before and after threshold (vertical line, T = threshold). The grey areas are the standard deviation of the accumulation rate curves. They are represented on the global species accumulation rate when no threshold appears, and on species accumulation rate before and after threshold lines when a threshold occurs.

Tables

ALT	Forest name	Forest composition	Project (Year)	HAR	RES
Highland	Ballons-Comtois	fir-beech	GNB (2010)	8 (16)	8 (15)
	Engins	spruce	GNB (2011)	5 (10)	4 (8)
	Lure	fir-beech	GNB (2011)	4 (8)	4 (8)
	Ventoux	fir-beech	GNB (2011)	5 (10)	5 (10)
	Ventron	fir-beech	GNB (2009)	4 (8)	4 (8)
Total Highland				**26 (52)**	**25 (49)**
Lowland	Auberive	beech	GNB (2009)	12 (24)	12 (24)
	Bois_du_Parc	oak-hornbeam	GNB (2011)	5 (5)	5 (5)
	Chizé	oak-beech	GNB (2010)	12 (24)	12 (24)
	Citeaux	oak-beech	GNB (2010)	6 (12)	6 (12)
	Combe-Lavaux	oak-beech	GNB (2010)	4 (8)	4 (8)
	Fontainebleau	oak-beech	GNB (2008)	13 (25)	12 (24)
	Haut-Tuileau	oak-hornbeam	GNB (2011)	7 (7)	7 (7)
	Rambouillet	oak-hornbeam	GNB (2012)	8 (16)	8 (16)
	Rambouillet	oak-hornbeam	RESINE (2006/2007)	44 (88)	16 (32)
	Verrières	oak-hornbeam	GNB (2012)	4 (8)	4 (8)
Total Lowland				**115 (217)**	**86 (160)**
Total				**141 (269)**	**111 (209)**

Table 1: Plot and trap distribution. Total trap number is between brackets. HAR= harvested plots; RES= reserve plots.

		GNB (y~a+b)			Rambouillet (y~a+b+c)					
		Forest reserve surface			Forest reserve surface			Nb patches		
		Rstot	Rsrar	Abrar	Rstot	Rsrar	Abrar	Rstot	Rsrar	Abrar
Lowland	Man	ns	ns	ns	ns	ns	ns	**2500 ***	ns	ns
	Unman	500 *	ns	ns	**2500 ****	ns	ns	ns	ns	2500 *
Highland	Man	2500 *	**500 ****	**1500 ****	NA	NA	NA	NA	NA	NA
	Unman	ns	ns	ns	NA	NA	NA	NA	NA	NA

Table 2: Summary of the best spatial scale models: effects of forest reserve surface area on total species richness and on rare species richness and abundance. The significance of the models is indicated after the best spatial scale effect (*;**; ***). For the particular case of Rambouillet, due to colinearity between forest reserve surface area and patch number, we only explored the 1500m; 2000m and 2500m spatial scales. The figures in bold indicate the detection of a threshold. Y = c(Rstot or Rsrar or Abrar); a = deadwood volume; b = forest reserve surface area; c = nb of patches.

Synthèse de l'article 7

e	Problématiques	Résultats Habitat	Résultats coléoptères saproxyliques	Points discutés	Questions soulevées	Perspectives d'étude	Conclusions
	1) En accord avec l'hypothèse de spillover, la proportion de surface forestière en réserve dans le paysage est-elle un bon estimateur pour prédire les variations locales de richesse spécifique dans les placettes exploitées? 2) En accord avec l'hypothèse d'effet de masse d'habitat, la quantité de réserves forestières dans le paysage affecte-t-elle la quantité d'espèces qui y sont retrouvées? 3) Ces différences sont-elles constantes entre forêts de plaine et forêts de montagne? 4) La totalité des espèces est-elle affectée, ou seulement les espèces rares? 5) Dans le cas particulier de la forêt de Rambouillet, le nombre de patches de réserves dans le paysage influence-t-il la richesse en espèces locale, une fois l'effet de la surface pris en compte?	Pas de mesures de variables d'habitat locales	**Jeu de données national:** En zone exploitée: *Richesse spécifique:* *En montagne: Toutes espèces:* Augmente avec la proportion de réserve dans le paysage (2.5km de rayon autour du piège); *Espèces rares*: Augmente avec la proportion de réserve dans le paysage (0.5km de rayon autour du piège. Seuil à 36.5% de réserves dans le paysage). *En plaine: Toutes espèces*: pas de réponse. *Espèces rares*: pas de réponse. *Abondance:* *En montagne: Toutes espèces:* pas de réponses. *Espèces rares:* Augmente avec la proportion de réserve dans le paysage (0.5km de rayon autour du piège. Seuil à 21.5% de réserves dans le paysage). En réserve: *Richesse spécifique:* *En montagne: Toutes espèces*: pas de réponse. *Espèces rares*: pas de réponse. *En plaine: Toutes espèces*: Augmente avec la proportion de réserve dans le paysage (0.5km de rayon autour du piège). *Espèces rares*: pas de réponse. **Jeu de données local (RAMBOUILLET):** En zone exploitée*: Richesse spécifique*: *Toutes espèces:* pas de réponse. *Espèces rares*: pas de réponse. *Abondance*: *Toutes espèces*: pas de réponse. *Espèces rares*: pas de réponse. *Nombre de patches de réserve:* *Richesse spécifique: Toutes espèces:* Augmente avec le nombre de patches de réserve dans le paysage (2.5km de rayon autour du piège. seuil à 2 patches de réserve dans le paysage). *Espèces rares*: pas d'effet. En réserve: *Richesse spécifique:* *Toutes espèces*: Augmente avec la proportion de réserve dans le paysage (2.5km de rayon autour du piège. Seuil à 20% de réserve dans le paysage). *Espèces rares:* pas de réponse. *Abondance: Toutes espèces*: pas de réponse. *Espèces rares:* pas de réponse. *Nombre de patches de réserve:* *Richesse spécifique: Toutes espèces:* pas de réponse. *Espèces rares*: pas de réponse. *Abondance*: *Toutes espèces:* pas de réponse. *Espèces rares*: Augmente avec le nombre de patches de réserve dans le paysage (2.5km de rayon autour du piège).	Ressources locales n'influencent pas forcément les assemblages observés. Phénomènes à l'échelle du paysage. Echelle spatiale considérées. Détection de seuils d'habitats pour des assemblages d'espèces. Disparition/fragmentation de l'habitat et diminution de la probabilité de survie des populations. Difficulté de considérer les zones exploitées comme non habitats pour les coléoptères saproxyliques. Débat SLOSS.	Effet de débordement (spillover)? Effet de quantité d'habitat (mass effect)? Différences de fonctionnement des réserves entre plaine et montagne? Les espèces de coléoptères répondent-elles de la même façon à la distribution spatiale des réserves dans le paysage?	Etude de l'évolution des populations dans les zones de réserve forestière.	Les réserves forestières ont un impact positif à la fois sur les populations qu'elles contiennent, mais également sur les populations des zones voisines.

Tableau 7 : Increasing the percentage of forest reserves in the landscape amplifies saproxylic beetle diversity both within and beyond reserve borders. Problématiques, résultats, éléments particuliers discutés, nouvelles problématiques posée, perspectives d'études à envisager et conclusions principales de l'article.

Partie II : 'Dette d'extinction' à l'échelle du paysage

Cette partie présente les éléments structurants qui ont conditionné notre réflexion sur l'importance de la prise en compte de la configuration passée du paysage sur les assemblages d'espèces observés actuellement. Nous y présentons des premiers éléments de matériels et méthodes pour une co-analyse menée avec l'université de České Budějovice.

Publication associée à cette partie : Article **8** (cf Tableau 2).

Evolution des différents éléments de la TTVB dans le paysage au cours du temps.

La surface forestière totale en France est en augmentation depuis 1830 (Cinotti, 1996 ; Dupouey *et al.,* 2007). Elle n'est cependant pas uniforme au sein du territoire national (IGN, 2014). Ces forêts de reconquête sont jeunes (moins de 200ans) et n'ont pas encore acquis les caractéristiques structurelles des stades terminaux de la sylvigenèse que sont les forts volumes et diversité de bois mort et dendromicrohabitats. Ces éléments récemment acquis par le paysage ne sont donc pas forcément en mesure d'assurer un habitat favorable aux espèces saproxyliques. L'augmentation de la surface forestière aurait alors un impact négatif sur les espèces dépendantes des milieux ouverts, sans pour autant favoriser les cortèges de coléoptères saproxyliques.

La forêt n'est pas l'unique habitat des espèces saproxyliques. Nous avons montré (ainsi que d'autres auteurs) que les éléments ligneux non forestiers participaient activement à la conservation des espèces saproxyliques. De plus, certaines espèces se sont révélées être des spécialistes des milieux non forestiers. Ces éléments peuvent être regroupés en trois groupes : (i) les bosquets et patches de bois de dimensions trop faibles pour être considérés en tant que forêts ; (ii) les structures linéaires. Ces structures sont constituées par des haies, des alignements d'arbres en bord de route, de bord de cours d'eau ; (iii) les arbres isolés, ou regroupés par petits groupes, mais ne formant pas un bois ou bosquet, et entourés d'espaces non boisés.

La plupart de ces éléments sont en régression depuis 1960 (Boureau *et al.,* 2005 ; Pointereau et Coulon, 2006). Le rythme de disparition des haies était élevé entre 1960 et 1980 (45.000 km/an) puis a diminué entre 1980 et 1990 (15.000km/an) et s'est stabilisé depuis (Pointereau et Coulon, 2006). On observe également un accroissement de l'âge des arbres constitutifs des haies alors que leur linéaire diminue (Pointereau, 2001). Cette situation n'est pas propre à la France et peut être constatée et en Pologne (Orlowski et Nowak, 2007) ou en République Tchèque (Miklin et Cizek, 2014).

Parmi ces éléments, le cas particulier des arbres solitaires ou des arbres de haies est à noter. Ces arbres étaient généralement traités de manière à fournir du bois de faible diamètre, sans provoquer la mort de l'arbre (Sebek *et al.,* 2013). Ce traitement particulier de têtard conduit à la formation de cavités, dendromicrohabitats particulièrement favorables à la diversité des organismes saproxyliques. Les cavités sont des dendromicrohabitats originaux qui se forment au bout d'un processus de plusieurs dizaines d'années. Une fois une cavité formée, elle peut -en fonction des

essences ligneuses sur lesquelles elle s'est formée- constituer un dendromicrohabitat pour un riche cortège d'espèces pendant des dizaines voire des centaines d'années.

Les organismes saproxyliques utilisant ces habitats sont particulièrement sensibles à la disparition de leur habitat et au phénomène de *dette d'extinction* (Ranius, 2007).

Influence de la structure passée du milieu sur les populations actuelles

La survie des populations d'organismes saproxyliques tient à la disponibilité en quantités suffisantes de leurs habitats. L'impact des activités humaines a largement réduit la quantité de forêts dans le paysage, et fragmenté cet habitat. Les patches d'habitat dans le paysage sont propices au fonctionnement en métapopulation des organismes. Dans ces milieux, les populations vont être tributaires d'un nombre variable de patches d'habitat dans le paysage. La connectivité des patches est un facteur clé pour assurer la survie de tels systèmes. Si la distance entre les patches est supérieure aux capacités de dispersion de l'espèce, ils ne seront pas connectés, et la quantité d'habitat disponible va diminuer. Si cette quantité d'habitat passe en dessous du seuil de survie de l'espèce, elle ne pourra pas à terme se maintenir dans le paysage et va disparaitre. La disparition d'espèces ne s'effectue donc pas forcément au même rythme que la disparition d'habitat. Ce phénomène est nommé « *dette d'extinction* » (Tilman *et al.,* 1994).

Des phénomènes de *dette d'extinction* et de réponses retardées dans le temps de la modification du milieu ont été mis en évidence pour plusieurs groupes taxinomiques :

Pour les plantes vasculaires, Cousins et Eriksson (2002) ont mis en évidence que les assemblages actuels étaient plus influencés par la gestion appliquée il y a 300ans que par la gestion actuelle. De manière similaire, Lindborg et Eriksson (2004) ont mis en évidence que la connectivité passée du milieu (entre 50 et 100 ans) était un paramètre expliquant les assemblages d'espèces actuels. Pour les lichens, la richesse en espèces était mieux expliquée par la structure passée (entre 110 et 140 ans) du milieu que présente (Ellis et Coppins, 2007). Pour les mousses, Snäll *et al,* (2004) ont montré que la distribution actuelle de *Neckera pennata* était mieux expliquée par la connectivité de son habitat il y a 20ans que sa connectivité actuelle. Pour les carabes, Petit et Burel (1998) ont montré que la distribution actuelle de *Abax parallellipipedus* était reliée à une structure du paysage telle qu'elle existait 40ans plus tôt. Pour les champignons saproxyliques, Paltto *et al,* (2006) ont montré que la densité d'espèces de champignons saproxyliques rares était plus influencée par le couvert forestier passé (120ans) que par d'autres variables relatives à la situation actuelle du milieu.

Pour les coléoptères saproxyliques, nous n'avons trouvé aucune référence qu'un effet de d*ette d'extinction* ait été détecté ou même recherché. Seuls Hanski et Ovaskainen (2002) ont mis en relation la proportion d'espèces rares disparues localement avec l'intensité de l'exploitation forestière. Ils ont trouvé que la proportion d'espèces disparues était significativement plus faible dans les paysages où l'activité d'exploitation forestière était la plus faible. Ceci suggère un effet de *dette d'extinction* mais ne le démontre pas directement. De la même façon, Siitonen et Saaristo (2000) ont mis en évidence que *Pytho kolwensis* ne se maintenait que sur des zones ayant eu un couvert arboré ces 150 dernières années. L'effet passé du paysage sur les populations actuelles suggère un effet de *dette d'extinction*, mais ne le démontre pas.

Problématique d'étude : Projet collaboratif franco-tchèque

L'évaluation de la contribution des éléments non forestiers de la TTVB à la conservation des organismes saproxyliques est encore mal connue. L'exploration que nous avons conduite révèle pourtant des structures essentielles au maintien d'espèces saproxyliques peu forestières (cf Chapitre III). Ces éléments forment à l'échelle du paysage un réseau plus ou moins connecté, qui tend à se fragmenter de plus en plus depuis 60ans en France (Cinotti, 1996), mais aussi dans d'autres pays européens (Miklin et Cizek, 2014). Dans ce contexte particulier, il est possible que les milieux actuels ne puissent déjà plus soutenir les populations d'espèces saproxyliques peu forestières qu'ils abritent. Ces populations seraient alors soumises à un effet de dette d'extinction. Ce constat amène à se poser les questions suivantes :

- La structuration passée du paysage influence-t-elle la composition et le nombre d'espèces des communautés de coléoptères saproxyliques observées aujourd'hui, en comparaison du paysage actuel ?

Matériel et méthodes

Nous allons co-analyser les données faunistiques issues de notre expérimentation menée sur la comparaison des assemblages en coléoptères saproxyliques entre arbres isolés et forêt et des données similaires en provenance de République Tchèque. Nous présentons ici des éléments de matériel et méthodes provisoires.

Sites d'étude : En France, deux paysages ateliers ont été échantillonnés, l'Allier et les Yvelines (cf Chapitre III). En république tchèque, ce sont trois paysages ateliers qui ont été retenus.

Coléoptères saproxyliques : Les assemblages de coléoptères saproxyliques ont été échantillonnés à l'aide de pièges à interception. Les pièges étaient suspendus à hauteur de la première charpentière. Le mélange conservateur ne contenait pas d'attractif. L'harmonisation de la nomenclature utilisée entre les différentes parties reste à conduire.

Densité passée et présente d'éléments de la TTVB non forestiers dans le paysage : L'évolution de la structuration spatiale du paysage repose sur l'analyse et la comparaison de photographies aériennes passées avec des photos récentes (en s'inspirant de Dubois *et al.,* 2009a). Dans le cas de la république tchèque, ces couches photographiques sont disponibles pour la totalité du pays (http://kontaminace.cenia.cz/). Elles remontent à environ 1938 et permettent d'estimer l'évolution du paysage (en particulier les éléments relatifs à la TTVB) au cours de ces 80 dernières années. En France, ces images sont disponibles (http://www.geoportail.gouv.fr/accueil) mais datant majoritairement des années 1950 et ne permettant d'estimer l'évolution du paysage que durant ces 60 dernières années. De plus, une étape de géoréférencement de ces images est à prévoir.

Nous considérons trois types de structures de la TTVB à cartographier : (i) la surface forestière. Le bois mort et les dendromicrohabitats sont des éléments essentiels pour la survie des organismes saproxyliques (Bouget *et al.,* 2014). Ces éléments ne sont pas répartis de manière uniforme au sein des forêts ou zones arborées, et ne sont pas de même nature en fonction de l'âge et de l'intensité

d'exploitation qui leur est associée. La caractérisation au niveau du paysage de ces éléments d'habitat particuliers est complexe et nécessite un lourd investissement de terrain. De ce fait, par souci pratique de faisabilité de l'étude, nous considérons toutes les surfaces forestières ou arborées dans le paysage comme d'égale qualité en tant qu'habitat pour les coléoptères saproxyliques. (ii) les structures linéaires. Ces structures sont constituées par des haies, des alignements d'arbres en bord de route, de bord de cours d'eau … (iii) les arbres isolés.

Les caractéristiques structurelles de chacun de ces éléments (dimensions minimales pour être considérés) restent cependant à préciser.

Variables : Nous envisageons d'étudier l'influence passé et présente de (i) la quantité d'habitat dans le paysage. Dans cette approche, chaque élément est converti en une surface d'habitat. (ii) la connectivité du milieu. Dans cette approche, chaque élément est également converti en surface d'habitat, mais les relations de distance entre les différents éléments et leur importance surfacique est conservée (Calabrese et Fan, 2004 ; Kupfer, 2012). L'estimation de la connectivité du milieu sera menée avec le logiciel FRAGSTAT (McGarigal *et al.,* 2004). La connectivité du milieu sera menée par une méthode basée sur la théorie des graphes (Newman, 2003). Cette méthode a été largement employée en biologie de la conservation ces dernières années (Carranza *et al.,* 2012 ; Decout *et al,* 2012). Comme toute méthode, elle n'est pas exempte de biais qu'il faudra prendre en compte (Moilanen, 2011).

Analyses envisagées : les différentes variables (en opposant passé/présent) seront mises en relation avec les caractéristiques des assemblages de coléoptères saproxyliques contactés (richesse spécifique, abondance, composition) grâce à des modèles linéaires mixtes ou généralisés. L'utilisation de ces modèles permet en effet une intégration des effets spatiaux inhérents à la structure de notre zone d'échantillonnage et des effets que cela peut avoir sur les cortèges d'espèces obtenus. Les analyses seront réalisées avec le logiciel R (R core Team, 2014).

Discussion générale

Discussion générale

Cette partie est dédiée à la synthèse générale des principaux résultats obtenus lors des différents travaux menés au cours de cette thèse (cf tableaux de synthèse individuels 3 ; 4 ; 5 ; 6 et 7). Cette synthèse va permettre d'émettre des propositions de mesures de gestion appliquées pour une meilleure conservation des coléoptères saproxyliques. Ces recommandations viendront soutenir les recommandations déjà préconisées par l'ONF (2009) dans les forêts publiques.

L'objectif de cette thèse était de mieux comprendre le rôle joué par les différents éléments de la TTVB à la conservation des espèces saproxyliques, aux échelles spatiales locales et paysagères. Nous avons décliné notre approche selon deux axes, correspondant aux deux échelles spatiales d'étude :

- **Quel est le rôle intrinsèque des éléments de la Trame de Très Vieux Bois à la conservation des coléoptères saproxyliques ?**
- **Quelle est l'influence de la quantité d'éléments de la TTVB dans le paysage sur les assemblages d'espèces de coléoptères saproxyliques ?**

Partie I : Synthèse des résultats et application à la mise en place des éléments de la TTVB en forêt publiques

I) Les éléments de la TTVB : une efficacité de conservation contrastée

En cas d'arrêt d'exploitation ou d'exploitation retardée (Ilots de vieillissement (IV)), les compartiments « bois mort » et « dendromicrohabitats » se régénèrent (Stokland *et al.,* 2012 ; Larrieu, 2014). Cette régénération apparait cependant différente en fonction des structures de conservation étudiées (Parmain *et al., in prep* [3] ; Bouget *et al.,* 2014 [7]).

I.1) Evolution du milieu après abandon d'exploitation ou rallongement du cycle sylvicole

L'arrêt ou le délai d'exploitation des peuplements forestiers entraine une croissance prolongée des arbres, provoquant une augmentation de leur diamètre (Parmain *et al., in prep* [3] ; Bouget *et al.,* 2014 [5]) mais également de leur surface totale à l'hectare Bouget *et al,* (2014) [5]. Les rapports entre volume de bois mort/volume total de bois (bois vivant + bois mort) sont supérieurs en zones non exploitées Bouget *et al,* (2014) [5]. Le volume total de bois mort ainsi que de dendromicrohabitats y est également supérieur. Au contraire, les zones ou l'exploitation finale du peuplement est retardée ne voient pas leurs volumes de bois mort ou de dendromicrohabitats augmenter Parmain *et al, in prep* [3].

I.1.1) Evolution de la densité et de la diversité du bois mort

Le bois mort n'est pas homogène, il est constitué de nombreux éléments, tels le boi mort sur pied ou au sol, de petit ou gros diamètre. Associés avec leur essence d'origine et leur degré de décomposition, ils constituent un grand nombre possibles de types de bois mort. Au sein des zones

exploitées, certains types de bois mort seront plus rares que d'autres. C'est par exemple le cas pour les bois morts de fort diamètre (Bouget *et al.,* (2014) [5]). Nous avons montré que le volume de bois mort représenté par les gros diamètres (debout ou au sol) étaient 8 fois plus important dans les zones non exploitées depuis au moins 30ans par rapport aux zones exploitées depuis moins de 30ans. Au contraire, les petits bois morts peu décomposés ont été retrouvés en nombre plus importants dans les zones exploitées (Moroni et Ryan, 2010). Nous avons observé que la diversité totale de bois mort en zones non exploitées était faiblement supérieure à la diversité retrouvée en zones exploitées (Bouget *et al.,* 2014 [5]). Cette observation peut s'expliquer par la courte période que représentent 30 années de non exploitation dans le contexte de forêts se développant sur plusieurs centaines d'années. Le volume et diversité de bois mort obtenus après 30/100 ans de non exploitation n'atteignent pas les volumes de bois mort qui peuvent être observés en forêts 'naturelles', qui n'ont jamais (ou très faiblement) été exploitées (Gilg, 2004 ; Bobiec, 2002).

Au contraire des réserves forestières, les stocks de bois mort n'étaient pas plus élevés dans les IV témoins que dans les IV arrivés à terme (Parmain *et al, in prep* [3]). Les structures d'habitat clés pour la conservation des coléoptères saproxyliques n'y étaient pas non plus présentes en quantités plus importantes. Cette non-modification du milieu peut être la résultante de deux facteurs : d'une part le maintien de l'exploitation forestière au cours du développement de l'IV, et d'autre part, la faible durée de l'extension de rotation. Pourtant, dans un souci de détectabilité d'effets potentiels, nous avons choisi d'étudier l'effet de l'équivalent de deux rotations d'aménagement forestier, soit un accroissement d'environ 10cm du diamètre des arbres, correspondant à environ 50ans de durée d'extension de rotation. De manière similaire, Lassauce *et al,* (2013) ont montré qu'en chênaie, le volume total de bois mort n'était pas plus important entre des placettes de 160 et 220 ans où l'activité forestière était maintenue. Nous avons mis en évidence que les volumes de bois mort étaient significativement plus élevés après 30 ans de non-exploitation en chênaie et en hêtraie (Bouget *et al.,* 2014 [5]). Meyer et Schmidt (2011) ont montré qu'en hêtraie, 9 ans de non-exploitation ans étaient suffisants pour doubler le volume de bois mort initialement présent. Il semblerait donc que ce soit le maintien des activités sylvicoles qui empêche toute régénération des stocks de bois mort.

En milieu extra-forestier, les volumes de bois mort observés aux alentours des arbres solitaires étaient bien inférieurs à ceux observés en forêt (Parmain et al. *in prep* [4]). La genèse du bois mort est principalement due (hors évènements catastrophiques) aux frottements entre branches d'arbres et à la compétition entre tiges (Siitonen, 2001). La cause principale de la diférence de volumes observés pourrait être la densité inférieure d'arbres à l'hectare et l'absence de sous-bois en milieu non forestier par rapport au milieu forestier. Cette densité d'arbres inférieure ne perpermet pas une dynamique de recrutement de bois mort aussi intensse qu'en forêt. Ce phénomène peut être amplifié par la pression qu'exercent les troupeaux d'animaux qui vont piétiner et déstructurer les branches mortes tombées au sol, ou au propriétaire privé qui va venir récolter ces branches.

I.1.2) Variations des stocks de dendromicrohabitats

Nous avons constaté une augmentation de la quantité et de la diversité de dendromicrohabitats dans les zones forestières non-exploitées depuis au moins 30 ans par rapport aux zones exploitées depuis moins de 30 ans (Bouget *et al.,* 2014 [5]). Certains dendromicrohabitats sont issus d'un processus

pouvant durer plusieurs dizaines d'années (cavités, voir Larrieu, 2014 et Sebek *et al.,* 2013). Au contraire, d'autres peuvent se former en un instant à la suite d'un évènement catastrophique (tempête), tels les houppiers brisés, les fentes, les plages d'écorces décollées. Au sein des parcelles exploitées, les arbres porteurs de dendromicrohabitats vont avoir une valeur marchande moins forte, car entrainant des défauts techniques dans le bois, des pourritures. La probabilité d'occurrence des dendromicrohabitats augmente donc avec le diamètre de l'arbre (Larrieu et Cabanettes, 2012).

Au sein des zones particulières que sont les IV, ni la quantité ni la diversité moyenne de dendromicrohabitats par très gros arbres (DBH>70cm) n'étaient impactées. Pourtant, la durée d'extension de rotation étudiée dépassait les 30 ans, durée suffisante permettant l'augmentation de la quantité et diversité de dendromicrohabitats en zone non exploitée (Bouget *et al.,* 2014 [5]). Là encore, à l'instar du bois mort, le maintien des activités sylvicoles ne permet pas l'augmentation de la quantité et diversité des dendromicrohabitats dans le peuplement.

Individuellement, les arbres solitaires portaient davantage de dendromicrohabitats que les arbres forestiers. Pourtant, la densité en dendromicrohabitats à l'hectare était identique en tre forêt et arbres solitaires. La diversité des dendromicrohabitats était également plus forte sur les arbres solitaires que sur les arbres forestiers. Au contraire de la quantité, la diversité en dendromicrohabitats n'était pas égale entre arbres forestiers et arbres solitaires. Les arbres solitaires possédaient une plus grande diversité de dendromicrohabitats à l'hectare (Parmain *et al, in prep* [4]). L'acquisition des dendromicrohabitats par les arbres solitaires va faire intervenir des phénomènes naturels et des phénomènes anthropiques. En plus d'être soumis aux perturbations naturelles 'classiques', les arbres solitaires sont exploités par l'Homme. Des besoins en bois de chauffage et d'affouage pour le bétail ont conduit l'homme à exploiter ces arbres sans causer leur mort, par opposition aux arbres forestiers (Sebek *et al.,* 2013). Ce traitement favorise la création de dendromicrohabitats (Sebek *et al.,* 2013) et explique la densité et diversité plus importante des dendromicrohabitats observée au niveau de l'arbre solitaire par rapport à l'arbre forestier.

La cinétique d'accumulation du bois mort et dendromicrohabitat semble donc différente en fonction des types forestiers et du contexte. Les peuplements de Hêtraie voient leur volume de bois mort augmenter plus rapidement qu'en Chênaie. Cependant, les périodes de temps sur lesquelles ces phénomènes ont été observés sont relativement courtes.

Quelle est la dynamique d'accumulation du bois mort et des dendromicrohabitats sur de longues périodes ? Cette accumulation est-elle dépendante du type de peuplement forestier ? La dynamique est-elle la même en forêt de plaine et de montagne ? Au bout de combien de temps de non exploitation les caractéristique structurelles du peuplement se rapprochent de celles des forêts naturelles ?

Quelles différences peut-il y avoir entre dynamique d'accumulation de bois mort et des dendromicrohabitats en zones forestières et non-forestières ?

I.2) Réponse des coléoptères saproxyliques aux variations locales d'habitat

Nous avons montré une faible réponse positive de la part des assemblages de coléoptères saproxyliques à l'arrêt de l'exploitation forestière sur une période d'environ 30 ans (Bouget *et al.,*

2014 [5]). Cet effet est largement dû à l'augmentation en quantité et diversité des éléments d'habitat clés de bois mort et de dendromicrohabitats favorables aux coléoptères saproxyliques (Bouget *et al.,* 2013 [6]). Cependant, indépendamment de l'amélioration de l'habitat, le facteur de durée de non-exploitation avait également un rôle explicatif de la composition des assemblages d'espèces et la richesse spécifique totale observée. Bien que cet effet soit faible, il suppose l'existence d'un phénomène temps-dépendant et non uniquement habitat-dépendant régissant la colonisation ou l'expansion des populations locales. Ce processus de colonisation temps-dépendant est à rapprocher du processus d'extinction (dette d'extinction) qui est lui aussi temps dépendant (Hanski et Ovaskainen, 2002). Dans les deux cas, le temps est un facteur clé, et les délais de réponse des organismes saproxyliques pourraient dépasser les périodes de temps actuellement étudiées.

Nous avons également mis en évidence la neutralité d'efficacité des IV pour la conservation des coléoptères saproxyliques. Les assemblages de coléoptères saproxyliques ne sont pas plus riches ou plus abondants dans les IV témoins que dans les IV à terme. De plus, aucune modification favorable de l'habitat en faveur des coléoptères saproxyliques n'est observée (Parmain et al. *in prep* [3]). Ces ilots arrivés à terme ne sont donc pas plus aptes à conserver la biodiversité que 25 ou 50 ans auparavant. Cette conclusion est valable pour les coléoptères saproxyliques mais pourrait être différente pour d'autres organismes saproxyliques. Si cela était avéré, alors ces zones constitueraient de grands pièges écologiques (Hedin *et al.,* 2008 ; Victorsson et Jonsell, 2012). Dans le cas particulier que représente les coléoptères saproxyliques et au vu des inconnues qui planent sur les délais de réponses aux modifications du milieu, nous ne concevons la conservation en faveur de ces organismes qu'à travers l'utilisation de structures fixes dans le temps et le paysage. Les structures temporaires de conservation sont au mieux inefficaces, et au pire vont à l'encontre des objectifs qu'elles souhaitent remplir.

Le changement de qualité d'habitat (augmentation ou diminution, échelle locale ou paysagère) favorables aux coléoptères saproxyliques peut s'effectuer assez rapidement, mais leur délai réponse est plus important, dépassant la dizaine d'années. Des phénomènes dépendants de stades plus avancés de l'évolution du milieu sont-ils à l'œuvre ? L'ancienneté du milieu forestier est il un paramètre déterminant pour les coléoptères saproxyliques ?

Nos résultats issus de la comparaison des assemblages des coléoptères saproxyliques des arbres forestiers avec des arbres solitaires sont conformes avec de précédentes études (Sverdrup-Thygeson, 2009). Nous avons mis en évidence une égale richesse d'espèces entre ces deux milieux. Pourtant, seule la moitié des espèces est commune entre les deux contextes. La recherche d'espèces indicatrices de chaque milieu a permis de mettre en évidence plusieurs espèces caractéristiques des arbres isolés (Parmain *et al., in prep* [4]). Ces résultats mettent en évidence l'intérêt que représentent les éléments non-forestiers (ici les arbres isolés) pour la conservation des coléoptères saproxyliques, car abritant des espèces non retrouvées en forêt.

Les arbres isolés ne sont pas les seuls éléments singuliers de la TTVB. Les ripisylves sont à bien des égards des milieux hautement favorables à la biodiversité saproxylique. Les habitats originaux fournis

par les ripisylves et les essences particulières qu'elles abritent pourraient constituer des habitats singuliers, non retrouvés en forêts et supportant des espèces spécifiques.

Quelle est la contribution des ripisylves à la conservation de la biodiversité saproxylique ? Cette contribution est-elle différente en fonction des contextes altitudinaux ? Quelle est la dynamique du bois morts et dendromicrohabitats en ripisylve ?

Nous avons montré que l'ouverture du milieu influence fortement les communautés de coléoptères saproxyliques (Parmain *et al.,* [4] ; Bouget *et al.,* 2013 [6]). Comme exprimé en discussion de l'article [4], cette relation a été observée par de nombreux auteurs et amène à des réflexions plus larges sur la structuration naturelle d'une forêt, en particulier la chênaie (Whitehouse et Smith, 2004). Cependant, l'influence positive de l'ouverture du milieu sur les coléoptères saproxyliques a principalement été mise en évidence par des études conduites à l'aide de pièges à interception. Cette méthode permet de contacter les espèces se déplaçant par le vol au sein des peuplements étudiées. Le nombre plus important d'espèces contactées dans les milieux plus ouverts pourrait donc être la résultante de deux facteurs : (i) Zones plus thermophiles, impliquant une activité plus importante des individus dans les zones ouvertes que dans les zones fermées, et donc, une plus grande détection d'individus et d'espèces. (ii) Les zones plus ouvertes pourraient être synonymes de perturbations locales induisant la création de bois mort, des blessures sur les arbres voisins et le développement de dendromicrohabitats. La plus grande ressource en habitats ainsi créée au sein des zones ouvertes pourrait également expliquer le plus grand nombre d'espèces qui y sont contactées.

L'ouverture du milieu en tant que paramètre d'habitat structurant les assemblages de coléoptères saproxyliques est-elle issue d'un biais méthodologique associé au piège à interception ?

II) Effets de masse et de débordement : Le rôle source des réserves forestières

Nous avons mis en évidence l'importance de la quantité de réserves forestières dans le paysage sur la richesse en espèces de coléoptères saproxyliques. La quantité de réserve dans le paysage semble agir de deux manières : par effet de masse (Fahrig, 2013) ; la richesse au sein des réserves augmente avec la proportion de réserve dans le paysage, par effet de débordement ; les espèces présentes dans les réserves atteignent des seuils populationnels qui produisent un nombre plus important d'individus dispersant dans les zones non-réserves. La relation entre la surface forestière en réserve et richesse ou abondance des espèces ne suit pas une relation linéaire. Nous avons mis en évidence des effets de seuils. Ces seuils sont de l'ordre de 20% de surface forestière en réserve dans le paysage. Passé ce seuil, l'accumulation des espèces (ou des individus) par le milieu est beaucoup plus importante. De plus, ces relations entre quantité de réserve et richesse en espèces ne sont pas identiques entre forêts de plaine et forêt de montagne (Parmain *et al., in prep* [7]).

Nos résultats mettent en évidence la nécessité de raisonner simultanément à plusieurs échelles spatiales pour assurer une conservation efficace de la biodiversité des coléoptères saproxyliques : En premier lieu, l'échelle locale, permet la compréhension des phénomènes régissant les assemblages locaux de coléoptères saproxyliques. Cette compréhension permet de mettre en place des mesures

conservatoires pertinentes à l'échelle locale, telles les arbres habitats, les ilots de sénéscence ou les réserves forestières.

En second lieu, l'échelle paysagère. Bien qu'ayant des effets positifs au niveau local (Bouget *et al.,* 2014 [5] ; Parmain *et al., in prep*[4]), les structures forestières de la TTVB (ici les réserves) ont des effets à l'échelle du paysage (Parmain *et al., in prep*[7]). Ces derniers semblent régis par des relations seuils entre espèces et quantité d'habitat. Ainsi, si la quantité de réserves dans le paysage forestier est en dessous des seuils détectés, bien que localement efficaces, ces réserves n'auront qu'un impact faible au niveau de la forêt. Au contraire, au-delà des seuils détectés, les effets locaux auront une répercussion sur la totalité du paysage forestier.

Les effets de masse et de débordement sont proposés pour expliquer le phénomène observé. Cependant, les protocoles mis en place pour nos études ne prévoyaient pas d'étudier ces phénomènes, ni de les mettre en évidence.

Comment mettre en évidence de tels effets ? À partir de quels niveaux populationnels interviennent-ils ? Sur quelles distances sont-ils effectifs ? Ces conditions sont-elles constantes entre différents types de peuplements et de conditions altitudinales ?

De manière plus large, la question de la répartition spatiale des différents éléments forestiers et non forestiers de la TTVB reste posée. Comment les espèces réagissent à divers degrés de fragmentation du paysage ? Le réseau crée par les différents éléments de la TTVB est-il fonctionnel ? Des efforts de conservation ciblés sur certains éléments sont-ils à fournir ?

III) Mesures de gestion en faveur de la biodiversité saproxylique

Nos résultats mettent en exergue plusieurs points clés pour l'amélioration des mesures conservatoires actuelles à prendre en faveur des coléoptères saproxyliques. Ces différents éléments sont traduits ici en applications pratiques à mettre en place par le gestionnaire soucieux d'améliorer les capacités d'accueil de 'sa' forêt pour la biodiversité des organismes saproxyliques.

III.1) Choisir efficacement les arbres habitats

Lors des différentes opérations sylvicoles, laisser un maximum d'arbres à faible valeur économique en place, ou les arbres présentant des dendromicrohabitats particuliers, tels les arbres à cavités. Les arbres présentatnt plusieurs types de dendromicrohabitats sont à privilégier. Cette étape est d'autant plus importante lors de la coupe définitive. Nous avons en effet montré que les assemblages d'espèces de coléoptères saproxyliques sont sensibles à la présence de dendromicrohabitats sur les arbres isolés (Parmain *et al, in prep*[4]). Bien que nos résultats soient fondés sur de arbres non forestiers, plusieurs études ont démontré l'importance du maintien d'arbres isolés en forêt au moment de la coupe définitive (Rosenvald et Lohmus, 2008 ; Hyvärinen *et al.,* 2005). Ces arbres peuvent être conservés individuellement ou par patches, chaque configuration ayant ses avantages et inconvénients. Des questions demeurent quand à la proportion d'arbres à conserver à l'hectare, pour fournir des objectifs de conservation sur lesquels le gestionnaire va pouvoir s'appuyer.

III.2) Ilots de vieux bois : vieillissement ou sénéscence ?

En France, les mesures de rallongement du cycle sylvicole ont été mises en place dans l'objectif de concilier production de bois de qualité et protection de la biodiversité (Jaret 2004 ; Sardin, 2008). Pourtant, le maintien des activités sylvicoles dans ces zones ne permet pas le développement d'un habitat de qualité pour l'accueil des organismes saproxyliques. Nous encourageons fortement les gestionnaires forestiers qui souhaitent mettre en place des ilots de vieux bois d'opter pour des ilots de sénescence plutôt que des ilots de vieillissement.

III.3) Quelle densité de réserves implanter ?

Nous avons montré que les relations habitat-espèce pour les coléoptères saproxyliques pouvaient être soumises à des effets de seuils importants. Nous avons conscience que des proportions avoisinant les 20% de surface forestière en réserve sont utopiques. Cependant, un maximum doit être fait pour continuer de générer des habitats favorables aux organismes saproxyliques pour assurer leur conservation et leur survie. L'évolution de la surface totale de réserves forestières en France est passée de 1.2% en 2000 à 6.7% en 2011 (ONF, 2011) avec 188 réserves de tous genres pour le seul territoire métropolitain (ONF Données internes 2011). Nous ne pouvons que saluer cette dynamique et inciter à aller toujours plus loin dans cette direction.

Partie II : Perspectives d'études sur la fragmentation spatiale des habitats des coléoptères saproxyliques

Nous proposons ici une démarche visant à modéliser précisément les relations existant entre fragmentation et connectivité du paysage et espèces de coléoptères saproxyliques. Cette approche se passe en deux temps. En premier lieu, estimer le degré de fragmentation de l'habitat au niveau du paysage étudié en fonction des groupes ciblés. En second lieu, se servir de modèles métapopulationnels en intégrant des valeurs précises de fragmentation du milieu et de distances de dispersion des espèces. Le but de l'approche est de produire des estimateurs fins permettant à un modèle métapopulationnel de produire des prédictions fiables.

Le degré de fragmentation de l'habitat est généralement estimé à partir de la théorie des graphes. Cette approche nécessite dans sa forme la plus basique de connaitre le nombre d'éléments d'habitat, leur surface et la distance qui les sépare pour estimer la fragmentation du milieu. Cependant, comme nous l'avons montré au cours de nos travaux, tous les éléments du paysage ne participent pas de la même manière à la conservation des espèces saproxyliques (Parmain *et al., in prep* [4]). Certaines espèces vont avoir besoin d'un couvert forestier pour survivre et se développer, alors que d'autres vont préférer des conditions ouvertes ou semi-ouvertes (Horak et Rebl, 2013). Les différents éléments d'habitat des espèces saproxyliques ne vont pas avoir la même valeur pour les différentes espèces du cortège. Il est donc primordial pour une prise en compte de la connectivité effective du paysage de connaitre précisément les capacités d'accueil des différentes structures qui le composent (Dubois *et al.,* 2009a). En fonction des échelles spatiales considérées, ces éléments peuvent être des pièces de bois mort, des forêts, des arbres isolés, des bosquets, des alignements … possédant tous une valeur d'accueil différente pour les espèces saproxyliques.

I) L'estimation de la fragmentation d'habitat dépend de la qualité des patches d'habitat

La mosaïque d'habitat s'exprime aux échelles locales et paysagères. A l'échelle locale, l'habitat des organismes saproxyliques va être constitué par le bois mort et les dendromicrohabitats répartis de manière non continue dans l'espace et le temps. A l'échelle paysagère, les surfaces boisées non forestières (parcs, bosquets, alignements de bords de route …) vont constituer autant d'habitats potentiels pour l'entomofaune saproxylique, comme nous l'avons mis en évidence pour le cas particulier des arbres isolés (Parmain et al. *in prep* [4]).

I.1) Différents types de bois mort pour différentes espèces

Le bois mort et les dendromicrohabitats sont des substrats évolutifs et spatialement structurés, qui constituent des taches d'habitat en turnover constant pour des organismes saproxyliques. Ils sont constitués d'éléments divers, chacun contribuant à la conservation d'une partie des espèces saproxyliques du milieu. La contribution relative de chacun de ces éléments est méconnue. L'évaluation de cette contribution individuelle doit être menée pour estimer efficacement le degré de fragmentation locale d'habitat. Cette évaluation peut à notre avis être atteinte par une approche méta-analytique. La question de recherche associée pourrait être : « Quelles sont les éléments de

bois mort les plus favorables à la conservation des espèces de coléoptères saproxyliques ? ». La multiplication récente des études qui ont mis en place des protocoles basés sur la mise en caisse d'émergence de pièces de bois mort de différents diamètres et degrés de décomposition variables pourrait permettre de répondre à cette question. Une approche similaire pourrait être conduite pour les dendromicrohabitats. Cependant, l'importance des dendromicrohabitats pour la conservation des espèces saprxyliques sont un sujet d'étude récent. Nous supposons qu'il n'y a pas encore suffisamment de publications disponibles pour mener une méta-analyse sur ce sujet.

Les résultats obtenus grâce à la méta-analyse pourront être validés par une approche expérimentale. Elle consisterait à mettre en place une cartographie à haute résolution spatiale de la ressource bois mort et dendromicrohabitat (arbres habitats, sénescents ou morts, bois mort) sur un ou deux massifs ateliers. Cette cartographie servira de base à la sélection de paysages de bois mort. Le degré de fragmentation spatiale sera estimé par les méthodes issues de la théorie des graphes en affectant des scores de qualités d'habitat différentes aux éléments bois mort issus de la méta-analyse conduite précédemment. Au sein de ces paysages contenant des densités et connectivités variables en types de bois mort, les assemblages de coléoptères saproxyliques seront échantillonnés. La relation entre deux types de prédicteurs (diversité en éléments d'habitat et connectivité du milieu) et de réponses (*i.e*. diversité et composition des communautés de coléoptères saproxyliques locales) sera analysée avec les outils classiques de l'écologie des communautés. Un biais pourrait être introduit par une forte corrélation entre volume de bois mort et fragmentation de l'habitat. Ce biais peut être évité en considérant des paires de paysage avec la même quantité d'habitat, mais avec des degrés de fragmentations variables. Nous supposons cependant que de tels paysages vont être complexes à trouver sur le terrain. Il pourrait être nécéssaire d'envisager un programme de recherche sur le long terme prévoyant la mise en place préalable de placettes expérimentales, sur lesquelles la répartition spatiale de différents types de bois mort serait contrôlée. Des expérimentations sur des paysages ateliers à large échelle sont en cours à travers le monde (Gustaffson *et al.,* 2012). Cependant, pour l'Europe, un seul projet existe et concerne la rétention de patches forestiers affectés par les incendies (projet FIRE, http://wanda.uef.fi/jarikouki/project_fire.htm) en milieu boréal.

I.2) Les ripisylves comme habitats privilégiés pour les coléoptères saproxyliques ?

Nous avons mis en évidence le rôle particulier joué par les réserves forestières ainsi que les arbres solitaires à la conservation des coléoptères saproxyliques à l'échelle du paysage (Bouget *et al.,* 2014 [5] ; Parmain *et al., in prep* [7]). Ces éléments ne sont pourtant pas les seuls à participer à la conservation des espèces saproxyliques. Peu d'études se sont focalisées sur les capacités d'accueil des différents éléments non forestiers de la TTVB pour les coléoptères saproxyliques. L'approche par méta-analyse ne semble donc pas pertinente pour cette partie. Pour des raisons de temps et de coût, l'estimation de la contribution à la conservation des coléoptères saproxyliques de la totalité des éléments non forestiers de la TTVB ne peut être menée, ou doit faire l'objet d'un travail dédié. Cependant, l'étude d'une structure particulière peut être envisagée, comme cela a été le cas pour nous. Nous proposons l'étude des éléments particuliers que sont les ripisylves car :

(i) la genèse de dendromicrohabitats favorables aux organismes saproxyliques y est accélérée (Bouget, 2008), ce qui en fait un excellent milieu refuge pour les organismes saproxyliques de haut niveau trophique. De plus, certaines espèces d'insectes saproxyliques se retrouvent exclusivement en

bordure de cours d'eau ou dans les milieux humides (Bouget, 2008). Les bois morts de larges diamètres n'y sont pas rares (Degerman *et al,* 2004). Dahlström *et al,* (2005) indiquent que les bois flottés peuvent rester peu dégradés pendant de longues périodes de temps, de l'ordre de plusieurs centaines d'années. Au contraire, Bouget (2008) indique que la dynamique des bois morts y est accélérée. La dynamique de décomposition du bois mort en ripisylve est encore mal comprise, mais conduit ponctuellement à d'importants volumes accumulés (Stockland *et al.,* 2012).

(ii) le rôle de corridor écologique de grande ampleur joué par les ripisylves (Gillies et StClair, 2008). En traversant de vastes étendues de paysage, elles sont de véritables « autoroutes » pour la dispersion des espèces. Naiman *et al,* (1993) souligne qu'en plus d'être un excellent corridor écologique, les ripisylves offrent de larges services écosystémiques, telle l'amélioration de la qualité des eaux.

Malgré ces caractéristiques clés pour la conservation des assemblages saproxyliques, peu de travaux sont menés sur les ripisylves (Dufour et Piégay, 2006). Nous avons effectué une recherche d'articles scientifiques sur ce sujet en utilisant les mots clés '« riparian forest » and saproxylic' dans des moteurs de recherche d'articles scientifiques. Sur un total de 39 résultats dans le moteur de recherche ScienceDirect (http://www.sciencedirect.com/), aucun article ne concernait la relation existant entre ripisylves et organismes saproxyliques. Sur le moteur de recherches SpringerLink (http://link.springer.com/), 17 résultats ont été détectés et parmi eux, un seul concernait le lien direct entre ripisylve et coléoptères saproxyliques (Della Roca *et al.,* 2014).

Nous envisageons l'étude de ripisylves ayant une large emprise riveraine, telles les ripisylves de l'Aube. Les dispositifs d'échantillonnage de la faune saproxylique seront installés à des distances croissantes du bord de la rive. Cette disposition va permettre de balayer un large gradient de conditions stationnelles disponible au sein des ripisylves, en passant des zones couramment inondées aux zones rarement submergées. Cette disposition particulière du dispositif d'échantillonnage va permettre d'avoir une vue d'ensemble des capacités d'accueil des ripisylves et pas uniquement des parties proches du bord des cours d'eau. Cette première approche sur les ripisylves de l'Aube devra être étendue par la suite à d'autres contextes géographiques, mais également de conformation de ripisylves. Des zones avec une faible épaisseur de végétation devront être comparées avec des zones voisines à forte épaisseur (possibilité impact de l'ambiance forestière, humidité, température, ensoleillement…). La difficulté de trouver ces zones va venir de la canalisation des fleuves et rivières en France (exemple, le Rhin), qui laissent peu de place aux ripisylves. Les ripisylves de bord de Loire ou d'Allier sont ainsi des secteurs d'études à privilégier, car encore globalement conservés, et géographiquement proches du centre d'études IRSTEA de Nogent sur Vernisson. Les parties plantées, cultivées et fréquemment exploitées des ripisylves telles les peupleraies devraient être évitées au cours des échantillonnages, car non représentatives de l'élément 'ripisylve'.

I.3) Ancienneté de l'habitat

La capacité d'accueil des éléments arborés de la TTVB va également dépendre de l'ancienneté du milieu. Siitonen et Saaristo (2000) ont montré qu'une espèce de coléoptère saproxylique *Pytho kolwensis* ne se développait que dans les placettes où la continuité forestière était assurée depuis plus de 150ans. Ces zones sont particulièrement rares en Europe. Après la dernière glaciation en

Europe, 80% de sa surface était recouverte de forêt (Gilg, 2004). Ces surfaces reliques, que l'on peut appeler des forêts anciennes, sont actuellement estimées à moins de 1% de la surface totale des forêts en Europe (Gilg, 2004). L'identification des forêts anciennes en France est difficile. Bien souvent les archives concernant la gestion des forêts ne remontent pas au-delà des cartes de Cassini (XVIIè au XIXè). Cependant, les forêts présentes sur ces cartes ont pu connaitre des déboisements totaux puis être replantées ou régénérées. Il faut pour cela les confronter avec les cartes d'état-major (XIXè siècle), plus précises (voir Dupouey *et al.,* 2007). Ainsi, pour des raisons principalement pratiques, seront considérées comme forêt ancienne les forêts présentes sur l'ensemble de ces cartes et existant encore de nos jours. Par opposition, une forêt ne répondant pas à cette définition sera considérée comme récente.

L'étude de cette problématique avait été envisagée lors de la création de cette thèse (Annexe 3). Pour des raisons de temps et de faisabilité, ce travail n'a pu être mené à bien. Il fait l'objet d'un travail de recherche connexe mené par Philippe Janssen à IRSTEA Grenoble. Les projets Distrafor et Forgeco sont également en lien avec les problématiques d'ancienneté forestière et de leur influence sur les assemblages d'espèces actuels. Les premiers résultats viennent confirmer l'importance déterminante de l'ancienneté de l'état boisé d'une forêt sur la structuration des assemblages de coléoptères saproxyliques (Bouget *et al., in press*).

I.4) Synthèse

La qualité d'habitat peut être mesurée de nombreuses façons, et à plusieurs échelles spatiales. Dans le cadre de la poursuite des travaux de thèse que nous avons menés, il nous apparait opportun d'étudier prioritairement la capacité d'accueil des ripisylves pour les coléoptères saproxyliques. Une meilleure compréhension de leur rôle de refuge potentiel et de corridor écologique est une voie possible pour aborder les problématiques de connectivité à l'échelle du paysage des différents éléments de la TTVB.

II) L'effet de la fragmentation sur les espèces dépend de leurs capacités de dispersion

L'habitat fragmenté que composent le bois mort en forêt mais également les différents éléments de la TTVB dans le paysage suggèrent un fonctionnement en métapopulation de espèces saproxyliques (Schroeder *et al.,* 2007). Ce type de fonctionnement ne semble cependant pas être applicable à la totalité des espèces saproxyliques (Driscoll *et al.,* 2010). Des modèles prédictifs de l'évolution de ces métapopulations dans le paysage ont été développés (Hanski, 1994). A partir du degré de fragmentation d'habitat dans le paysage, des capacités de dispersion connues ou estimées des espèces cibles, et de leur taux de colonisation et survie, l'évolution de la viabilité des métapopulations au cours du temps peut être simulée. Ces simulations sont actuellement utilisées comme outil d'aide à la conservation de plusieurs espèces de coléoptères saproxyliques (Oleksa *et al.,* 2013). Ils se doivent d'être particulièrement précis quant aux prédictions qu'ils vont émettre, toute erreur pouvant mener à des mesures de gestion ne permettant pas la survie de l'espèce cible

dans le temps. Cette qualité de prédiction va reposer sur la qualité des données de base intégrées dans le modèle.

La capacité de dispersion des espèces saproxyliques est mal connue, et n'est vaguement disponible que pour quelques espèces (Ranius, 2006). De plus, les phénomènes de dispersion au sein d'une même espèce peuvent être sexe-dépendants (Watson, 2003, Dubois *et al.,* 2009b, Bouget *et al., in press*). Ceci pose le problème de la colonisation de nouveaux patches d'habitat dans un environnement fortement fragmenté (Davy-Bowker, 2002 ; Gyllenstrand et Seppa, 2003). Il est nécessaire d'acquérir des connaissances plus détaillées sur les capacités de dispersion des espèces pour permettre des modélisations fines d'évolution des métapopulations dans le paysage.

Nous allons présenter différentes méthodes disponibles pour mesurer les capacités de dispersion des espèces. Il est évident que la mise en place de la totalité des méthodes au sein d'un seul travail ne pourra être menée.

II.1) Méthodes directes de mesure des capacités de vol

II.1.1) Suivis de dispersion individuels *in natura*

La technique de capture marquage-recapture (CMR) a été principalement utilisée pour estimer des tailles de populations (Chiari *et al.,* 2012). Cette approche permet également d'estimer les distances de dispersion d'organismes particuliers, à des fins conservatoires (Drag *et al.,* 2011 ; Svensson *et al,* 2011) ou de protection vis-à-vis de ravageurs (Bancroft et Smith, 2005). Des études de CMR ont été menées en Espagne sur deux espèces de coléoptères saproxyliques particulièrement faciles à observer, *Cerambyx welensi* et *Prinobius myardi* (Lopez-Pantoja *et al.,* 2011). Des distances de dispersion maximales ont ainsi pu être observées pour ces deux espèces. Le marquage d'espèces de cette taille ne pose pas de problèmes particuliers. Des pastilles numérotées peuvent être appliquées sur les élytres, ou les élytres peuvent être perforés pour créer un marquage propre à chaque individu (Unruh et Chauvin, 1993). Ces individus ne peuvent être directement capturés sur le terrain sans introduire le biais de l'âge de l'insecte, des ressources qu'il a consommées et du temps qu'il lui reste à vivre et donc, la distance potentielle qu'il peut parcourir. Pour cela, nous privilégions la piste de l'élevage. Certaines espèces de coléoptères saproxyliques sont couramment et facilement élevées (http://www.insectes.org/opie/elevages-insectes.html) et peuvent être obtenues en grand nombre assez rapidement (quelques mois). Le facteur de pollution génétique des populations locales induit par l'introduction de souches issues d'élevage peut être évité si ces souches sont prélevées au sein des paysages d'étude.

Les espèces cibles pour l'expérimentation de CMR devront avoir des caractéristiques supposées de dispersion contrastées, et des modalités d'élevage maitrisées, simples à mettre en œuvre. De bons voiliers pouvant parcourir de grandes distances (*Cetonia aurata* ?) des voiliers médiocres mais pouvant largement disperser (*Dorcus parallelepipedus* ?) des mauvais voiliers dispersant peu (*Ceruchus chrysomelinus* ?). Une réflexion reste à conduire quant au choix des espèces à considérer.

Dans le cadre d'une expérimentation forestière, la recapture manuelle des espèces ne nous semble pas envisageable, la surface à parcourir par l'expérimentateur étant trop grande. Selon nous, l'utilisation de pièges spécifiques aux espèces cibles est indispensable pour mener à bien ce genre d'études. L'utilisation de pièges tels les pièges à interception contacteraient un trop grand nombre

d'espèces associées, constituant une destruction non-nécessaire de nombreux individus d'espèces non ciblées. Une alternative consisterait alors à utiliser des pièges non létaux pour les individus, mais implique une grande disponibilité de l'expérimentateur pour relever fréquemment les pièges.

Des zones de recapture où les espèces seront attirées de manière active à l'aide de phéromones ou d'un substrat particulier sont à envisager (Svensson *et al.,* 2011). Ces manipulations impliquent d'avoir accès à un grand nombre d'individus initiaux, car les taux de recapture même en utilisant des phéromones sont faibles (Zolubas et Byers, 1995).

II.1.2) Colonisation de substrats pièges

Un substrat piège correspond par exemple à une fructification de *Fomitopsis* pour *Bolitophagus reticulatus* ou *Neomida haemorrroidalis* (Coleoptera, Tenebrionidae). Cette méthode permet d'estimer les capacités de dispersion des espèces en tenant compte des conditions environnementales (Ranius *et al.,* 2011). En prenant en compte les propriétés du milieu et les caractéristiques paysagères de la zone d'étude, il est possible de mettre en évidence des phénomènes de dispersion sélectives en direction par exemple de zones refuges telles les réserves, ou au contraire des mouvements d'émigration depuis de telles structures (effet de débordement, voir expérimentation de Jonsson et Norlander, (2006)). Les distances de dispersion alors observées seraient pas uniquement dépendantes des capacités propres de l'insecte, mais reliées à la structuration de l'environnement. Ces données permettraient de ne pas surestimer les capacités de dispersion effectives des espèces considérées obtenues par exemple à l'aide de manèges de vol. Des substrats pièges plus complexes peuvent être mis en place, telles des cavités artificielles (Hilszczanski *et al,* 2014 ; Jansson *et al.,* 2009).

Dans le cadre d'évaluation de distances de dispersion d'espèces particulières, l'utilisation de phéromones peut être couplée au piège substrat (Svensson et Larsson, 2008). Elles permettent de stimuler le comportement dispersif des espèces par rapport aux substrats pièges simples, mais sont alors susceptibles de fournir des données de dispersion contraintes, ne traduisant pas forcément les dispersions qui s'effectuent de manière réelle.

II.1.3) Capacités de vol des espèces en laboratoire

Le manège de vol est un moyen efficace de connaitre les capacités physiologiques de vol des espèces étudiées. Ils peuvent s'adapter à des insectes de toutes tailles. Des manèges de vol ont par exemple été mis en place avec succès pour *Osmoderma eremita* (Dubois *et al.,* 2009b), *Monochamus galloprovincialis* (David *et al.,* 2013), *Bolitophagus reticulatus*, *Neomida haemorroidalis* (Jonsson, 2003) et *Ips sexdentatus* (Jactel et Gaillard, 1991). Les avantages principaux de cette méthode sont la relative facilité de mise en œuvre, le contrôle associé aux individus (sexe, poids, taille, âge …), et le faible coût de la manipulation.

II.2) Un indicateur de la capacité de vol : la charge alaire

Cet indice se base sur le poids d'un individu mis en relation avec la surface d'une de ces ailes (Gibb *et al.,* 2006). Le rapport entre les deux fournit un coefficient dit de charge alaire. Ce coefficient

représente la pression des ailes exercée sur l'air pour soutenir le poids du corps. Plus ce coefficient sera faible, plus la capacité de dispersion potentielle de l'insecte sera élevée.

Cette méthode à l'avantage de pouvoir être mise en œuvre avec des échantillons d'insectes issus de piégeage. Ainsi, les charges alaires des espèces du milieu pourront être mesurées et mises en relation avec de variables environnementales locales (Bouget *et al., in press*). En revanche, il n'est pas possible d'estimer la distance effective de dispersion d'une espèce par cette méthode. De plus, Bouget *et al,* (*in press*) ont montré que la charge alaire pouvait varier au sein des espèces. Les individus se retrouvant dans les patches de forêts récentes avaient une charge alaire plus faible que ceux retrouvés dans les patches de forêts anciennes proches. Ce résultat milite en faveur de l'utilisation de la charge alaire comme indicateur des capacités de dispersion des espèces, car suffisament sensible pour détecter des différences populationelles.

Au contraire des méthodes directes, l'approche par la mesure de la charge alaire ne permet pas d'obtenir une distance de dispersion métrique, mais seulement un comparatif possible de capacités de dispersions relatives entre plusieurs individus, espèces, populations … La validation de la pertinence de la mesure de charge alaire pour les coléoptères saproxyliques doit être menée. La mise en relation de la charge alaire d'individus dont les capacités de dispersion ont été préalablement mesurées à l'aide de moulins de vol pourrait être une piste de recherche.

La mesure de la surface alaire s'expose à des contraintes pratiques que sont la fragilité de la pièce anatomique en question, et sa possible variation inter individus. L'utilisation de paramètres moins délicats à mesurer (longueur d'élytre) est actuellement à l'étude.

II.3) Synthèse

Les capacités de dispersion des coléoptères saproxyliques peuvent être estimées de plusieurs façons. Nous pensons que le développement de la mesure de charge alaire des espèces est une piste prometteuse. Elle est relativement rapide à mettre en œuvre et peut être appliquée à des échantillons de projets antérieurs en lien avec la fragmentation ou l'ancienneté du site. Si cette méthode s'avère représentative des capacités de dispersion des espèces, il sera alors plus rapide et moins contraignant d'estimer les capacités de dispersion des espèces de coléoptères saproxyliques que par des méthodes de mesures sur individus vivants ou nécéssitant de lourdes expérimentations de terrain.

Bibliographie

Bibliographie

A

Akçakaya, H.R., Mills, G., Doncaster, C.P., (2007). The role of metapopulations in conservation. in Key Topics in Conservation Biology, Pages 64-84. D.W. Macdonald and K. Service, editors. Blackwell Publishing.

Alexander, K.N.A., (2008). Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. *Revue Écologie (Terre Vie)*, **63**: 1-5.

Andrén, H., (1994). Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with DifferentProportions of Suitable Habitat: A Review. *Oikos*, **71**: 355-366.

Andrén, H., (1996). Population Responses to Habitat Fragmentation: Statistical Power and the Random Sample Hypothesis. *Oikos*, **76**: 235-242.

Angers, V.A., Messier, C., Beaudet, M., Leduc, A., (2005). Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *Forest Ecology and Management,* **217**: 275–293.

Anon, (2003). *Saproxylic Organism*. P 5 in: Mason, F. Nardi G. Tisato, M. (eds). *Proceedings of the International Symposium "Dead wood: a key to biodiversity*", Mantova, May 29th-31st 2003. Sherwood 95, Suppl. 2.

ARE, (2014). *Catalogue des Coléoptères de France*. Perpignan, Association Roussillonnaise d'Entomologie éd., 1056p.

Arnaud, P.M., Emig, C., (1986). *La population, unité fonctionnelle de la biocœnose*. Colloque CNRS "Biologie des Populations", Lyon sept. 1986.

B

Baguette, M., (2004). The classical metapopulation theory and the real, natural world: A critical appraisal. *Basic and Applied Ecology*, **5**: 213–224.

Bancroft, J.S., Smith, M.T., (2005). Dispersal and influences on movement for *Anoplophora glabripennis* calculated from individual mark-recapture. *Entomologia Experimentalis et Applicata,* **116**: 83–92.

Bässler, C., Müller, J., (2010). Importance of natural disturbance for recovery of the rare polypore *Antrodiella citrinella* Niemelä & Ryvarden. *Fungal Biology*, **114**: 129-133.

Baum, K.A., Haynes, K.J., Dillemuth, F.P., Croninthe, J.T., (2004). The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**: 2671–2676.

Beaulieu, M., Thierry, A.M., Handrich, Y., Massemin, S., leMaho, Y., Ancel, A., (2010). Adverse effects of instrumentation in incubating Adélie penguins (*Pygoscelis adeliae*). *Polar Biology,* **33**:485–492.

Bergmann, K.O., Jansson, N., Claesson, K., Palmer, M.W., Milberg, P., (2012). How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. *Forest Ecology and Management,* **265**: 133–141.

Bigot, C., (2014). *Cinématique de décomposition et rôle de protection pare-pierres du bois mort: le cas des rémanents.* Université de Grenoble 235p.

Bobiec, A., (2002). Living and dead wood in the Bialowieza forest : suggestions for restoration management. *Forest Ecology and Management,* **165**: 125-140.

Boncina, A., (2000). Comparison of Structure and Biodiversity in the Rajhenav Virgin Forest Remnant and Managed Forest in the Dinaric Region of Slovenia. *Global Ecology and Biogeography*, **9**: 201-211.

Bouget, C., (2007). Enjeux du bois mort pour la conservation de la biodiversité et la gestion des forêts. *RDV techniques ONF,* **16**: 55-59.

Bouget, C., (2008). Diversité des insectes des forêts humides: Enjeux de conservation et de gestion. Les insectes en zones humides continentales, Monthieux (Dombes, Ain), Fondation Pierre Vérots.

Bouget, C., Brin, A., Tellez, D., Archaux, F., (*in press*) Intraspecific variations in dispersal ability of saproxylic beetles in fragmented forest patches. *Oecologia*

Bouget, C., Brustel, H., Brin, A., Valladares, L., (2009). Evaluation of window flight traps for effectiveness at monitoring dead wood-associated beetles: the effect of ethanol lure under contrasting environmental conditions. *Agricultural and Forest Entomology*, **11**: 143–152.

Bouget, C., Brustel, H., Nagelaisen, L.M., (2005). Nomenclature des groupes écologiques d'insectes liés au bois : synthèse et mise au point sémantique. *Comptes Rendus Biologies,* **328**: 936–948.

Bouget, C., Brustel, H., Zagatti, P., (2008). The French Information System on Saproxylic Beetle Ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation status. *Revue d'Ecologie (suite de La Terre et la Vie),* 33-36.

Bouget, C., Duelli, P., (2004). The effects of windthrow on forest insect communities: a literature review. *Biological Conservation,* **118**: 281–299.

Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., (2013). In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation,* **22**: 2111–2130.

Bouget, C., Lassauce, A., Jonsell, M., (2011). Effects of fuelwood harvesting on biodiversity — a review focused on the situation in Europe. *Canadian Journal of Forest Research*, **42**: 1421–1432.

Bouget, C., Parmain, G., Gilg, O., Noblecourt, T., Nusillard, B., Paillet, Y., Pernot, C., Larrieu, L., Gosselin, F., (2014). Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? *Animal Conservation*, **17**: 342–353.

Boureau, J.G., Foyer-Bénos, C., Lucas, S., (2005). Le paysage forestier vu du ciel. *L'If, IFN* **10**: 12.

Brudvig, L.A., Damschen, E.I., Tewksbury, J.J., Haddad, N.M., Levey, D.J., (2009). Landscape connectivity promotes plant biodiversity spillover into non-target habitats*. Proceedings of the National Acasdemy of Sciences of the United States of America,* **106**, 9328-9332.

Brustel, H., (2001). *Coléoptères saproxyliques et valeur biologique des forêts française*. Institut National Polytechnique. Toulouse. 297p.

Buse, J., Assman, T., Friedman, A.L.L., Rittner, O., Pavlicek, T., (2013) Wood-inhabiting beetles (Coleoptera) associated with oaks in a global biodiversity hotspot: a case study and checklist for Israel. *Insect Conservation and Diversity*, **6**: 687–703.

Bütler, R., Angelstam, P., Ekelund, P., Schlaepfer, R., (2004). Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. *Biological Conservation*, **119**: 305–318.

C

Calabrese, J., Fagan, W.F., (2004). A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment,* **2**: 529–536.

Carlson, A., (2000). The effect of habitat loss on a deciduous forest specialist species: the White-backed Woodpecker (*Dendrocopos leucotos*). *Forest Ecology and Management,* **131**: 215-221.

Carpaneto, G.M., Mazziotta, A., Coletti, G., Luiselli, L., Audisio, P., (2010). Conflict between insect conservation and public safety: The case study of a saproxylic beetle (*Osmoderma eremita*) in urban parks. *Journal of Insect Conservation,* **14**: 555–565.

Carranza, M., D'Alessandro, E., Saura, S., Loy, A., (2012). Connectivity providers for semi-aquatic vertebrates: the case of the endangered otter in Italy. *Landscape Ecology*, **27**:281–290.

Chen, Y., Chen, L., Stergiou, K.I., (2003). Impacts of data quantity on fisheries stock assessment. *Aquatic Science,* **65**: 92–98.

Chiari, S., Marini, L., Audisio, P., Ranius, T., (2012). Habitat of an Endangered Saproxylic Beetle, *Osmoderma eremita*, in Mediterranean Woodlands. *Ecoscience*, **19**: 299-307.

Christensen, M., Hahn, K., Mountford, E.P., Odor, P., Standovar, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., (2005). Dead wood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecology and Management,* **210**: 267–282.

Cinotti, B., (1996). Evolution des surfaces boisés en France: proposition de reconstitution depuis le début du XIXe siècle. *Revue Forestière Française,* **XLVIII**: 547-562.

Conseil de l'Europe, (2003). *Déclaration sur le réseau écologique paneuropéen*. 5ème Conférence Ministérielle. Kiev, Ukraine.

Cousins, S.A.O., Vanhoenacker, D., (2011). Detection of extinction debt depends on scale and specialization. *Biological Conservation*, **144**: 782–787.

D

Dahlström, N., Jönsson, K., Nilsson, C., (2005). Long-term dynamics of large woody debris in a managed boreal forest stream. *Forest Ecology and Management*, **210**: 363–373.

David, G., Giffard, B., Piou, D., Jactel, H., (2013). Dispersal capacity of Monochamus galloprovincialis, the European vector of the pine wood nematode, on flight mills. *Journal of Applied Entomology,* **138**: 566–576.

Davy-Bowker, J., (2002). A mark and recapture study of water beetles (Coleoptera: Dytiscidae) in a group of semi-permanent and temporary ponds. *Aquatic Ecology,* **36**: 435–446.

Decout, S., Manel, S., Miaud, C., Luque, S., (2012). Integrative approach for landscape-based graph connectivity analysis: a case study with the common frog (*Rana temporaria*) in human-dominated landscapes. *Landscape Ecology*, **27**: 267–279.

Degerman, E., Sers, B., Törnblom, J., Angelstam, P., (2004). Large Woody Debris and Brown Trout in Small Forest Streams: Towards Targets for Assessment and Management of Riparian Landscapes. *Ecological Bulletins,* **51**: 233-239.

Della Roca, F., Stefanelli, S., Pasquaretta, C., Campanaro, A., Bogliani, G., (2014). Effect of deadwood management on saproxylic beetle richness in the floodplain forests of northern Italy: some measures for deadwood sustainable use. *Journal of Insect Conservation,* **18**: 121–136.

Déry, S., Leblanc, M., (2005). *Lignes directrices pour l'implantation des ilots de vieillissement rattachées à l'objectif sur le maintien de forêts mûres et surannées - Partie II : intégration à la planification forestière.* Gouvernement du Québec. Québec, ministère des Ressources naturelles et de la Faune Direction de l'environnement forestier: 18p.

Drag, L., Hauck, D., Pokluda, P., Zimmermann, K., Cizek, L., (2011). Demography and Dispersal Ability of a Threatened Saproxylic Beetle: A Mark-Recapture Study of the Rosalia Longicorn (*Rosalia alpina*). *PLoS ONE,* **6**: e21345. doi:10.1371/journal.pone.0021345.

Driscoll, D.A., Kirpatrick, J.B., McQuillan, P., Bonham, K.J., (2010). Classic metapopulations are rare among common beetle species from a naturally fragmented landscape. *Journal of Animal Ecology*, **79**: 294–303.

Dubois, G., (2009). Écologie des coléoptères saproxyliques : Biologie des populations et conservation d'*Osmoderma eremita* (Coleoptera : Cetoniidae). U.M.R. 6553 ECOBIO. Rennes, Université de Rennes1: 216.

Dubois, G.F., Vignon, V., Delettre, Y.R., Rantier, Y., Vernon, P., Burel, F., (2009a). Factors affecting the occurrence of the endangered saproxylic beetle *Osmoderma eremita* (Scopoli, 1763) (Coleoptera: Cetoniidae) in an agricultural landscape. *Landscape and Urban Planning*, **91**: 152–159.

Dubois, G.F., LeGouar, P.J., Delettre, Y.R., Brustel, H., Vernon, P., (2009b) Sex-biased and body condition dependent dispersal capacity in the endangered saproxylic beetle *Osmoderma eremita* (Coleoptera: Cetoniidae). *Journal of Insect Conservation*, **14**:679–687.

Dubourdieu, J., (1997). *Manuel d'aménagement forestier*. ONF, Lavoisier Tech & Doc. 243p.

Dufour, S., Piégay, H., (2006). Forêts riveraines des cours d'eau et ripisylves : spécificités, fonctions et gestion. *Revue Forestière Française,* **LVIII**: 339-350.

Dugger, K.M., Ballard, G., Ainley, D.G., Barton, K.J., (2006) Effects of flipper bands on foraging behavior and survival of Adélie penguins (*Pygoscelis adeliae*). *The Auk,* **123**: 858-869.

Dunn, R.R., (2000). Isolated trees as foci of diversity in active and fallow fields. *Biological Conservation*, **95**: 317-321.

Dupouey, J.L., Bachacou, J., Cosserat-Mangeot, R., Aberdam, S., Vallauri, D., Chappart, G., Corvisier de Villèle, M.A., (2007). Vers la réalisation d'une carte géoréférencée des forêts anciennes de France. *Monde des Cartes,* **191**: 85-98.

E

Ehrlich, P.R., (1988). *The loss of diversity: causes and consequences*. Biodiversity. E. O. Wilson. Washington D.C., National Academic press: 21-27.

Ellis, C.J., Coppins, B.J., (2007). Changing climate and historic-woodland structure interact to control species diversity of the *'Lobarion'* epiphyte community in Scotland. *Journal of Vegetation Science,* **18**: 725-734.

Elton, C., (1966). *Dying and dead wood*, In: Elton, C. (Ed): *The patterns of animal communities*. New York. pp. 279-305 In: Dajoz, R. (1998) *Les insectes et la forêt. Rôle et diversité des insectes dans le milieu forestier*. Tech & Doc Lavoisier, Paris.

Engen, S., Lande, R., Saether, B.E., (2002). The Spatial Scale of Population Fluctuations and Quasi-Extinction Risk. *The American Naturalist,* **160**: 439-451.

F

Fahrig, L., (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics,* **34**: 487-515.

Fahrig, L., (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography,* **40:** 1649–1663.

FAO, (2011). *Situation des forêts du monde 2011*. Rome, 176p.

FAO, (2012). *Situation des forêts du monde 2012.* Rome, 52p.

Fischer, J., Stott, J., Law, B.S., (2010). The disproportionate value of scattered trees. *Biological Conservation,* **143**: 1564–1567.

Fridman, J., Walheim, M., (2000). Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management,* **131**: 23-36.

G

Gering, J.C., Crist, T.O., Veech, J.A., (2003). Additive Partitioning of Species Diversity across Multiple Spatial Scales: Implications for Regional Conservation of Biodiversity. *Conservation Biology,* **17**: 488–499.

Gibb, H., Hilszczanski, J., Hjaltén, J., Danell, K., Ball, J.P., Pettersson, R.B., Alinvi, O., (2008). Responses of parasitoids to saproxylic hosts and habitat: a multi-scale study using experimental logs. *Oecologia*, **155**: 63–74.

Gibb, H., Hjälten, J., Ball, J.B., Pettersson, R.B., Landin, J., Alvini, O., Danell, K., (2006). Wing loading and habitat selection in forest beetles: Are red-listed species poorer dispersers or more habitat-specific than common congenerics? *Biological Conservation,* **132**: 250-260.

Gilg, O., (2004). *Forets à caractère naturel. Caractéristiques, conservation et suivi*. Réserves Naturelles de France, Gestion des milieux et des Espèces, Cahiers techniques n°74. 96p.

Gillies, C.S., StClair, C.C., (2008). Riparian Corridors Enhance Movement of a Forest Specialist Bird in Fragmented Tropical Forest. *Proceedings of the National Academy of Sciences of the United States of America,* **105**: 19774-19779.

Götmark, F., Söderlundh, H., Thorell, M., (2000). Buffer zones for forest reserves: opinions of land owners and conservation value of their forest around nature reserves in southern Sweden. *Biodiversity and Conservation,* **9**: 1377–1390.

Gouix, N., (2011). Gestion forestière et Biodiversité, les enjeux de conservation d'une espèce parapluie : *Limoniscus violaceus* (Coleoptera). Sorbonne, Thèse 258p.

Gouix, N., Brustel, H., (2012). Emergence trap, a new method to survey *Limoniscus violaceus* (Coleoptera: Elateridae) from hollow trees. *Biodiversity and Conservation,* **21**: 421-436.

Gove, A.D., Majer, J.D., Rico-Gray, V., (2009). Ant assemblages in isolated trees are more sensitive to species loss and replacement than their woodland counterparts. *Basic and Applied Ecology,* **10**: 187-195.

Green, P., Peterken, G.F., (1997). Variation in the amount of dead wood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. *Forest Ecology and Management,* **98**: 229-238.

Gresslier, N., Renaud, J.P., Chauvin, C., (1995). Les forêts subnaturelles de l'arc alpin français. Réflexion méthodologique pour un recensement et une typologie des principales forêts alpines peu transformées par l'homme. *Revue Forestière Française*, **XLVII**: 241-254.

Grove, S.J., (2002a) Saproxylic Insect Ecology and the Sustainable Management of Forests. *Annual Review of Ecology and Systematics,* **33**: 1-23.

Grove, S.J., (2002b) Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. *Ecological Indicators,* **1**: 171-188.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lohmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygesson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., (2012). Retention Forestry to Maintain Multifunctional Forests: A World Perspective. *BioScience*, **62**: 633-645.

Gyllenstrand, N., Seppa, P., (2003). Conservation genetics of the wood ant, Formica lugubris in a fragmented landscape. *Molecular Ecology,* **12**: 2931-2940.

H

Halpern, C.B., Spies, T.A., (1995). Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications,* **5**: 913-934.

Hanski, I., (1994). A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**: 151-162.

Hanski, I., (2004). Metapopulation theory, its use and misuse. *Basic and Applied Ecology*, **5**: 225–229.

Hanski, I., Ovaskainen, O., (2002). Extinction debt at extinction threshold. *Conservation Biology*, **16**: 666–673.

Hedin, J., Isacsson, G., Jonsell, M., Komonen, A., (2008). Forest fuel piles as ecological traps for saproxylic beetles in oak. *Scandinavian Journal of Forest Research*, **23**: 348-357.

Hilszczanski, J., Jaworski, T., Plewa, R., Jansson, N., (2014). Surrogate tree cavities: boxes with artificial substrate can serve as temporary habitat for *Osmoderma barnabita* (Motsch.) (Coleoptera, Cetoniinae). *Journal of Insect Conservation*, **18**: 855–861.

Holland, J.D., Bert, D.G., Fahrig, L., (2004). Determining the Spatial scale of species responses to habitat. *BioScience*, **54**, 227-233.

Holland, J.D., Fahrig, L., Cappuccino, N., (2005). Body size affects the spatial scale of habitat/beetle interactions. *Oikos,* **110**: 101-108.

Holub, S.M., Spears, J.D.H., Lajtha, K., (2001). A reanalysis of nutrient dynamics in coniferous coarse woody debris. *Canadian Journal of Forest Research,* **31**: 1894-1902.

Horak, J., Rébl, K., (2013). The species richness of click beetles in ancient pasture woodland benefits from a high level of sun exposure. *Journal of Insect Conservation*, **17**:307–318.

Horak, J., Vodka, S., Pavlicek, J., Boza, P., (2013). Unexpected visitors: flightless beetles in window traps. *Journal of Insect Conservation*, **17**: 441-449.

Hyvärinen, E., Kouki, J., Martikainen, P., Lappalainen, H., (2005). Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *Forest Ecology and Management*, **212**: 315–332.

I

IGN (2014) *La forêt en chiffres et en cartes.* Paris, 29p.

J

Jactel, H., Gaillard, J., (1991). A preliminary study of the dispersal potential of Ips sexdentatus (Boern) (Col., Scolytidae) with an automatically recording flight mill. *Journal of Applied Entomology,* **112**: 138-145.

Jansson, N., Ranius, T., Larsson, A., Milberg, P., (2009). Boxes mimicking tree hollows can help conservation of saproxylic beetles. *Biodiversity and Conservation*, **18**: 3891–3908.

Jaret, P., (2004). *Guide des sylvicultures. Chênaie atlantique*. ONF, Paris, 335p.

Jones, E.W., (1945). The structure and reproduction of virgin forest of the North temperate zone. *New Phytologist,* **44**:130-148.

Jonsell, M., (2004). Old park trees: A higly desirable ressource for both history and beetle diversity. *International Society of Arboriculture,* **30**: 238-244.

Jonsell, M., (2007). Effects on biodiversity of forest fuel extraction, governed by processes working on a large scale. *Biomass and Bioenergy*, **31**: 726–732.

Jonsell, M., (2012). Old park trees as habitat for saproxylic beetle species. *Biodiversity and Conservation*, **21**: 619–642.

Jonsson, M., (2003). Colonisation ability of the threatened tenebrionid beetle Oplocephala haemorrhoidalis and its common relative *Bolitophagus reticulatus*. *Ecological Entomology*, **28**: 159–167.

Jonsson, M., Norlander, G., (2006) Insect colonisation of fruiting bodies of the wood-decaying fungus Fomitopsis pinicola at different distances from an old-growth forest. *Biodiversity and Conservation,* **15**: 295–309.

K

Kaila, L., (1993). A new method for collecting quantitative samples of insects associated with decaying wood fungi. *Entomologica Fennica*, **4**: 21-23.

Kirby, K.J., Thomas, R.C., Key, R.S., McLean, I.F.G., Hodgetts, N., (1995). Pasture-woodland and its conservation in Britain. *Biological Journal of the Linnean Society,* **56**: 135-153.

Kirby, K.J., Webster, S.D., Anctzak, A., (1991). Effects of forest management on stand structure and the quantity of fallen dead wood: some British and Polish examples. *Forest Ecology and Management,* **43**: 167-174.

Komonen, A., Penttilä, R., Lindgren, M. Hanski, I., (2000) Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, **90**: 119-126.

Korpel, S., (1995). *Die Urwälder der Westkarpaten*. Stuttgart, Gustav Fischer Verlag.

Krauss, D., Krumm, F., (eds) (2013). *Integrative approaches as an opportunity for the conservation of forest biodiversity*. European Forest Institute. 284p.

Krusic, R.A., Yamasaki, M., Neefus, C.D., Pekins, P.J., (1996). Bat Habitat Use in White Mountain National Forest. *The Journal of Wildlife Management*, **60**: 625-631.

Kupfer, J.A., (2012). Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape. *Progress in Physical Geography,* **36**: 400-420.

Kuussaari, M., Bommarco, R., Heikkinen, R., Helm, A., Krauss, J., Lindborg, R., Öckinger, Erik., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., Ingolf, S.D., (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution,* **24**: 564-571.

L

Lachat, T., Bütler, R., (2007). *Gestion des vieux arbres et du bois mort. Ilots de sénescence, arbres-habitat et métapopulations saproxyliques*. Mandat de l'Office fédéral de l'environnement. Lausanne: 87p.

Laiho, R., Prescott, C.E., (1999). The contribution of cwd to C, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Canadian Journal of Forest Research,* **29**: 1592-1603.

Lamarre, G.P.A., Molto, Q., Fine, P.V.A., Baraoto, C., (2012). A comparison of two common flight interception traps to survey tropical arthropods. *ZooKeys*, **216**: 43–55.

Larrieu, L., (2014). *Les dendro-microhbitats: facteurs clés de leur occurrence dans les peuplements forestiers, impact de la gestion et relations avec la biodiversité taxonomique.* Université de Toulouse, 115p.

Larrieu, L., Cabanettes, A., (2012). Species, live statut, and diameter are important tree features for diversity and abundance of tree-microhabitats in subnatural montane beech-fir forests. *Canadian Journal of Forest Research,* **42**: 1433-1445.

Larrieu, L., Cabanettes, A., Gonin, P., Lachat, T., Paillet, Y., Winter, S., Bouget, C., Deconchat, M., (2014). Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: A life-cycle approach to biodiversity. *Forest Ecology and Management*, **334**: 163–173.

Larrieu, L., Cabanettes, A., Delarue, A., (2012). Impact of silviculture on dead wood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. *European Journal of Forest Research*, **131**:773–786.

Larrieu, L., Gonin, P., (2008). L'indice de biodiversité potentielle (ibp) : une méthode simple et rapide pour évaluer la biodiversité potentielle des peuplements forestiers. *Revue Forestière Française*, **LX**: 727-748.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., (2011). Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, **11**: 1027–1039.

Lassauce, A., Larrieu, L., Paillet, Y., Lieuthier, F., Bouget, C., (2013). The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation lengths in a French oak high forest. *Insect Conservation and Diversity,* **6**: 396–410.

Leather, S., (2005). *Insect sampling in forest ecosystems*. Methods in Ecology, Blackwell Publishing, 303p.

Leroy, B., Pétillon, J., Gallon, R., Canard, A., Ysnel, F., (2012). Improving occurrence-based rarity metrics in conservation studies by including multiple rarity cut-off points. *Insect Conservation and Diversity*, **5**: 159-168.

Lindborg, R., Eriksson, O., (2004). Historical landscape connectivity affects present plant species diversity. *Ecology,* **85**: 1840–1845.

Linder, P., Elfving, B., Zackrisson, O., (1997). Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management,* **98**: 17-33.

Lohmus, A., Lohmus, P., Remm, J., Vellak, K., (2005). Old-growth structural elements in a strict reserve and commercial forest landscape in Estonia. *Forest Ecology and Management,* **216**: 201–215.

Lopez-Pantoja, G., Dominguez, L., Sanchez-Osorio, I., (2011). Analysis of *Prinobius myardi* Mulsant population dynamics in a Mediterranean cork oak stand. *Annales de la Société Entomologique de France*, **47**: 260-268.

Lucey, J.M., Hill, J.K., (2012). Spillover of Insects from Rain Forest into Adjacent Oil Palm Plantations. *Biotropica*, **44**: 368-377.

Lumsden, L.F., Bennett, A.F., (2005). Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia. *Biological Conservation,* **122**: 205-222.

Luyssaret, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., Grace, J., (2008). Old-growth forests as global carbon sinks. *Nature*, **455**: 213-215.

Lyons, K.G., Brigham, C.A., Traut, B.H., Schwartz, M.W., (2005). Rare Species and Ecosystem Functioning. *Conservation Biology*, **19**: 1019-1024.

M

MacArthur, R.H., Wilson, E.O., (1967, repinted 2001). *The theory of island biogeography*. Princeton University Press. XV+203p.

MacInerny, G., Travis, J.M.J., Dythamd, C., (2007). Range shifting on a fragmented landscape. *Ecological informatics,* **2**: 1-8.

Maguire, D.A., Halpern, C.B., Phillips, D.L., (2007). Changes in forest structure following variable-retention harvests in Douglas-fir dominated forests. *Forest Ecology and Management*, **242**: 708–726.

Manning, A.D., Fisher, J., Lindenmayer, D.B., (2006). Scattered trees are keystone structures – Implications for conservation. *Biological Conservation*, **132**: 311-321.

Maquet, J., Letellier, C., Aguirre, L.A., (2007). Global models from the Canadian lynx cycles as a direct evidence for chaos in real ecosystems. *Journal of Mathematical Biology,* **55**: 21–39.

Marage, D., Lempérière, G., (2005). The management of snags: A comparison in managed and unmanaged ancient forests of the Southern French Alps. *Annals of Forest Science*, **62**: 135–142.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., Rauh, J., (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation*, **94**: 199-209.

Maupeou, G., (1996). La chênaie méditerranéenne dans les forêts publiques du Languedoc-Roussillon. *Forêt méditerranéenne,* **XVII**: 196.

McGarigal, K., Cushman, S.A., Ene, E., (2012). FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst.

Meyer, P., Schidt, M., (2011). Accumulation of dead wood in abandoned beech (Fagus sylvatica L.) forests in northwestern Germany. *Forest Ecology and Management*, **261**: 342–352.

Michel, A.K., Winter, S., (2009). Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. *Forest Ecology and Management*, **257**: 1453–1464.

Miklin, J., Cizek, L., (2014). Erasing a European biodiversity hot-spot: Open woodlands, veteran trees and mature forests succumb to forestry intensification, succession, and logging in a UNESCO Biosphere Reserve. *Journal for Nature Conservation,* **22**: 35– 41.

Moilanen, A., (2011). On the limitations of graph-theoretic connectivity in spatial ecology and conservation. *Journal of Applied Ecology,* **48**: 1543–1547.

Molina, R., Marcot, B.G., Lesher, R., (2006). Protecting Rare, Old-Growth, Forest-Associated Species under the Survey and Manage Program Guidelines of the Northwest Forest Plan. *Conservation Biology*, **20**: 306–318.

Moroni, M.T., Ryan, D.A.J., (2010). Deadwood abundance in recently harvested and old Nova Scotia hardwood forests. *Forestry,* **83**: 219-227.

Mourey, J.M. Touroult, J., (2010). *Les arbres à conserver pour la biodiversité Comment les identifier et les désigner* ? Fiche Technique-Biodiversité. ONF, Paris. 3: 7.

Müller, J., Bussler, H., Kneib, T., (2008). Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *Journal of Insect Conservation,* **12**:107–124.

Müller, J., Noss, R.F., Bussler, H., Bralndl, R., (2010). Learning from a ‘‘benign neglect strategy” in a national park: Response of saproxylic beetles to dead wood accumulation. *Biological Conservation*, **143**: 2559–2569.

Müller, J., Horton, T., Pretzsch, H., (2007). Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech *Fagus sylvatica* L. *Forest Ecology and Management,* **242**: 297–305.

N

Nageleisen, L.M., Bouget, C., coord., (2009). L’étude des insectes en forêt : méthodes et techniques, éléments essentiels pour une standardisation. Synthèse des réflexions menées par le groupe de travail « Inventaires Entomologiques en Forêt » (Inv.Ent.For.). *Les Dossiers Forestiers* n°**19**, Office National des Forêts, 144p.

Naiman, R.J., Decamps, H., Pollock, M., (1993). The Role of Riparian Corridors in Maintaining Regional Biodiversity. *Ecological Applications,* **3**: 209-212.

Newman, M.E.J., (2003). The structure and function of complex networks. *SIAM Revue,* **45**: 167–256.

Nieto, A., Alexander, N.A., (2010). *European RedList of saproxylic beetles*. Luxembourg: Publications Office of the European Union. 39p.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Lider, P., Ljungberg, H., Mikusinski, G., Ranius, T., (2003). Erratum to ‘‘Densities of large living and dead trees in old-growth temperate and boreal forests’. *Forest Ecology and Management,* **178**: 355–370.

Nordén, B., Ryberg, M., Götmark, F., Olausson, B., (2004). Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biological Conservation*, **117**: 1–10.

Novotny, V., Basset, Y., (2000). Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, **89**: 546-572.

O

Odor, P., Heilmann-Cjausen, J., Christensen, M., Aude, E., van Dort, K.W., Piltaver, A., Siller, I., Veerkamp, M.T., Walleyn, R., Standovar, T., van Hess, A.F.M., Kosec, J., Matocec, N., Kraigher, M.T., Grebenc, T., (2006). Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biological Conservation*, **131**: 58-71.

Ohsawa, M., (2007). The role of isolated old oak trees in maintaining beetle diversity within larch plantations in the central mountainous region of Japan. *Forest Ecology and Management,* **250**: 215-226.

Okland, B., Bakke, A., Hagvar, S., Kvamme, T., (1996). What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity and Conservation*, **5**: 75-100.

Oldeman, R.A.A., (1990). *Forests: Elements of Silvology*. Berlin, Springer-Verlag.

Oleksa, A., Chybicki, I.J., Gawronski, R., Svensson, G.P., Burczyk, J., (2013). Isolation by distance in saproxylic beetles may increase with niche specialization. *Journal of Insect Conservation*, **17**: 219–233.

ONF, (2009). *Conservation de la biodiversité dans la gestion courante des forêts publiques*. INS-09-T-71: 11.

ONF, (2011). *Bilan patrimonial des Forêts Domaniales hors DOM.* ONF Paris, 180p.

ONF, (2013). *Rapport d'activité et développement durable*. ONF Paris, 138p.

Orlowski, G., Nowak, L., (2007). The importance of marginal habitats for the conservation of old trees in agricultural landscapes. *Landscape and Urban Planning*, **79** : 77–83.

P

Paltto, H., Nordén, B., Götmark, F., Franc, N., (2006). At which spatial and temporal scales does landscape context affect local density of Red Data Book and Indicator species? *Biological Conservation*, **133**: 442-454.

Parmain, G., Dufrêne, M., Brin, A., Bouget, C., (2013). Influence of sampling effort on saproxylic beetle diversity assessment: implications for insect monitoring studies in European temperate forests. *Agricultural and Forest Entomology,* **15**: 135–145.

Parmain, G., Bouget, C., et al. (in prep). Extended rotations in French oak forests do not enhance saproxylic beetle diversity.

Parmain, G., Bouget, C., et al. (in prep). Are solitary trees keystone structures for saproxylic biodiversity conservation? .

Parmain, G., Bouget, C., et al. (in prep). Increasing the percentage of forest reserves in the landscape amplifies saproxylic beetle diversity both within and beyond reserve borders.

Parrotta, J.A., Francis, J.K., Knowles, O.H., (2002). Harvesting intensity affects forest structure and composition in an upland Amazonian forest. *Forest Ecology and Management,* **169**: 243–255.

Parviainen, J., Bücking, W., Vandekerkhove, K., Schuck, A., Päivinen, R., (2000). Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4). *Forestry*, **73**: 107-118.

Penttilä, R., Siitonen, J., Kuusinen, M., (2004). Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. *Biological Conservation*, **117**: 271–283.

Perrin, H., (1946). Etudes statistiques sur les taillis sous futaie. *Annales de l'école nationale des eaux et forêts et de la station de recherches et expériences,* **10**: 1-102.

Pétillon, J., Courtial, C., Canard, A., Ysnel, F., (2007). First assessment of spider rarity in Western France. *Revista Ibérica de Aracnología*, **15**: 105-113.

Petit, S., Burel, F., (1998). Effects of landscape dynamics on the metapopulation of a ground beetle (Coleoptera, Carabidae) in a hedgerow network. *Agriculture, Ecosystems and Environment,* **69**: 243-252.

Pointereau, P., (2001). *Evolution du linéaire de haies en France durant ces 40 dernières années : l'apport et les limites des données statistiques*. Hedgerows of the world, their ecological functions in different lanscapes. Birmingham.

Pointereau, P., Coulon, F., (2006). *La haie en France et en Europe : évolution ou régression, au travers des politiques agricoles.* PREMIÈRES RENCONTRES NATIONALES DE LA HAIE CHAMPÊTRE. Auch.

Poulin, J.F., Villard, M.A., Edman, M., Goulet, P.J., Eriksson, A.M., (2008). Thresholds in nesting habitat requirements of an old forest specialist, the Brown Creeper (*Certhia americana*), as conservation targets. *Biological Conservation*, **141**: 1129-1137.

Procter, D., Harding, P.T., (2003). *Red Lists for Invertebrates: their application at different spatial scales – practical issues, pragmatic approaches.* JNCC Report No. 367 Proceedings of INCardiff.

R

R Core Team., (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rahman, M.M.; Frank, G., Ruprecht, H., Vacik, H., (2008). Structure of coarse woody debris in Lange-Leitn Natural Forest Reserve, Austria*. Journal of Forest Science,* **54**: 161-169.

Rameau, J.C., (1999). Accrus, successions végétales et modèles de dynamique linéaire forestière. Revue EAT thématique, 33-48.

Ranius, T., (2006). Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. *Population Ecology,* **48**: 177–188.

Ranius, T., (2007). Extinction risks in metapopulations of a beetle inhabiting hollow trees predicted from time series. *Ecography,* **30**: 716-726.

Ranius, T., Caruso, A., Jonsell, M., Juutinen, A., Thor, G., Rudolphi, J., (2014). Dead wood creation to compensate for habitat loss from intensive forestry. *Biological Conservation*, **169**: 277–284.

Ranius, T., Fahrig, L., (2006). Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. *Scandinavian Journal of Forest Research,* **21**: 201-208.

Ranius, T., Kindvall, O., (2006). Extinction risk of wood-living model species in forest landscapes as related to forest history and conservation strategy. *Landscape Ecology,* **21**:687–698.

Ranius, T., Martikainen, P., Kouki, J., (2011). Colonisation of ephemeral forest habitats by specialized species: beetles and bugs associated with recently dead aspen wood. *Biodiversity and Conservation,* **20**: 2903–2915.

Ranius, T., Nilsson, S.G., (1997). Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees. *Journal of Insect Conservation,* **1**: 193–204.

Ranius, T., Roberge, J.M., (2011). Effects of intensified forestry on the landscape-scale extinction risk of dead wood dependent species. *Biodiversity and Conservation*, **20**:2867–2882.

Reunanen, P., Mönkkönen, M., Nikula, A., (2001). Managing boreal forests landscapes for flying squirrels. *Conservation Biology,* **14**: 1218-226.

Reunanen, P., Mönkkönen, M., Nikula, A., Hurme, E., Nivala, V., (2004). Assessing landscape thresholds for the Siberian flying squirrel. *Ecological Bulletins,* **51**: 277–286.

Roberge, J.M., Angelstam, P., Villard, M.A., (2008). Specialised woodpeckers and naturalness in hemiboreal forests – Deriving quantitative targets for conservation planning. *Biological Conservation*, **141**: 997-1012.

Roland, J., Taylor, P.D., (1997). Insect parasitoid species respond to forest structure at different spatial scales. *Nature,* **386**: 710-713.

Rosenvald, R., Lohmus, A., (2008). For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management*, **255**: 1–15.

Rougerie, R., Lopez-Vaamonde, C., Barnouin, T., Delnatte, J., Moulin, N., Noblecourt, T., Nusillard, B., Parmain, G., Soldati, F., Bouget, C., (under review) PASSIFOR: A reference library of DNA barcodes for French saproxylic beetles (Insecta, Coleoptera). *Biodiversity Data Journal*.

Rouveyrol, P., (2009). *Caractérisation d'un ilot idéal de vieux arbres en forêt de montagne*. ENGREF. AgroParisTech. Paris: 185p.

Rowse, G., Thomas, K.C., Waterhouse, B.R., Knight, M.E., (2011). Increased bumblebee abundance along the margins of a mass flowering crop: evidence for pollinator spill-over. *Oikos,* **120**: 1618–1624.

Rudolphi, J., Gustafsson, L., (2005). Effects of forest-fuel harvesting on the amount of deadwood on clear-cuts. *Scandinavian Journal of Forest Research,* **20**: 235-242.

Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., Zielinski, W.J., (eds). (1994). *The Scientific Basis for Conserving Forest Carnivores: American Marten, Fisher, Lynx and Wolverine in the Western United States.* Gen. Tech. Rep. RM-254. Ft. Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 184p.

Russ, G.R., Alcala, A.C., (2011). Enhanced biodiversity beyond marine reserve boundaries: the cup spillith over. *Ecological Applications*, **21**: 241-250.

S

Sabovljevic, M., Vujicic, M., Sabovljevic, A., (2010). Diversity of saproxylic bryophytes in old-growth and managed beech forests in the Central Balkans. *Plants Biosystems,* **144**: 234-240.

Sahlin, E., Schroeder, L.M., (2010). Importance of habitat patch size for occupancy and density of aspen-associated saproxylic beetles. *Biodiversity and Conservation*, **19**: 1325–1339.

Sang, A., Teder, T., Helm, A., Pärtel, M., (2010). Indirect evidence for an extinction debt of grassland butterflies half century after habitat loss. *Biological Conservation,* **143**: 1405–1413.

Sardin, T., (2008). *Guide des sylvicultures. Chênaies continentales*. ONF, Paris. 455p.

Schoen, J.W., (1990). Bear Habitat Management: A Review and Future Perspective. *Bears: Their Biology and Management,* **8**: 143-154.

Schroeder, L.M., Ranius, T., Ekbom, B., Larsson, S., (2007). Spatial occurrence of a habitat-traking saproxylic beetle inhabiting a managed forest landscape. *Ecological Applications,* **17**: 900–909.

Schuck, A., Parviainen, J., Bücking. W., (1994). A review of approaches to forestry research on structure, succession and biodiversity of undisturbed and semi-natural forests and woodlands in Europe. *European Forest Institute Working Paper*, **3**:1-62.

Schwartz, M.W., (1999). Choosing the Appropriate Scale of Reserves for Conservation. *Annual Review of Ecology and Systematics,* **30**: 83-108.

Sebek, P., Altman, J., Platek, M., Cizek, L., (2013). Is Active Management the Key to the Conservation of Saproxylic Biodiversity? Pollarding Promotes the Formation of Tree Hollows. *PLoS ONE,* **8**: e60456. doi:10.1371/journal.pone.0060456.

Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F., Meriguet, B., Micas, L., Noblecourt, T., Rose, O., Velle, L., Bouget, C., (2012) A test for assessment of saproxylic beetle biodiversity using subsets of "monitoring species". *Ecological Indicators,* **20**: 304–315.

Siitonen, J., (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletin,* **49**: 11-41.

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management,* **128**: 211–225.

Siitonen, J., Saaristo, L., (2000). Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological Conservation*, **94**: 211-220.

Similä, M., Kouki, J., Martikainen, P., (2003). Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management*, **174**: 365–381.

Sippola, A.L., Siitonen, J., Kallio, R., (1998). Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish lapland. *Scandinavian Journal of Forest Research,* **13**: 204–214.

Sitzia, T., Trentanovi, G., Dainese, M., Gobbo, G., Lingua, E., Sommacal, M., (2012). Stand structure and plant species diversity in managed and abandoned silver fir mature woodlands. *Forest Ecology and Management,* **270**: 232–238.

Snäll, T., Hagström, A., Rudolphi, J., Rydin, H., (2004). Distribution pattern of the epiphyte Neckera pennata on three spatial scales / importance of past landscape structure, connectivity and local conditions. *Ecography,* **27**: 757-766.

Speight, M.C.D., (1989). *Les invertébrés saproxyliques et leur protection.* Collection sauvegarde de la nature. Strasbourg, Conseil de l'Europe. 42: 77.

Spies, T., Franklin, J., (1988). Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology*, **69**: 1689–1702.

Stenbacka, F., Hjaltèn, J., Hilszczanski, J., Dynesius, M., (2010). Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecological Applications,* **20**: 2310–2321.

Stokland, J., Meyeke, E., (2008). The saproxylic database: an emerging overview of the biological diversity in dead wood. *Revue Ecologie (Terre Vie) supplément*, **10**: 37-48.

Stokland, J., Siitonen, J., Jonsson, B.G., (2012). *Biodiversity in dead wood*. Cambridge university press, 509p.

Stokland, J.N., Tomter, S.M., Söderberg, U., (2004). *Development of Dead Wood Indicators for Biodiversity Monitoring: Experiences from Scandinavia*. EFI Proceedings, 207-226.

Sturtevent, B.R., Bissonette, J.A., Long, J.N., (1996). Temporal and spatial dynamics of boreal forest structure in western Newfoundland: silvicultural implications for marten habitat management. *Forest Ecology and Management,* **87**: 13-25.

Svensson, G.P., Larsson, M.C., (2008). Enantiomeric Specificity in a Pheromone–Kairomone System of Two Threatened Saproxylic Beetles, *Osmoderma eremita* and *Elater ferrugineus*. *Journal of Chemistry in Ecology*, **34**: 189–197.

Svensson, G.P., Sahlin, U., Brage, B., Larsson, M.C., (2011). Should I stay or should I go? Modelling dispersal strategies in saproxylic insects based on pheromone capture and radio telemetry: a case study on the threatened hermit beetle *Osmoderma eremita*. *Biodiversity and Conservation*, **20**:2883–2902.

Svensson, L., Grant, P.J., Mullarney, K., Zetterström, D., (2014). *Le guide ornitho. Le guide le plus complet des oiseaux d'Europe, d'Afrique du Nord et du Moyen-Orient : 900 espèces*. Delachaux et Niestlé.

Sverdrup-Thygeson, A., (2009). Oaks in Norway: Hotspots for red-listed beetles (Coleoptera). In: Buse, J., Alexander, K.N.A., Ranius, T., Assmann, T. (Eds). *Saproxylic beetles – Their role and diversity in European woodland and tree habitats.* Proceedings of the 5th Symposium and Workshop on the Conservation of saproxylic Beetles. Pensoft, Sofia-Moscow, 235p.

Sverdrup-Thygesson, A., Birkemoe, T., (2009) What window traps can tell us: effect of placement, forest openness and beetle reproduction in retention trees. *Journal of Insect Conservation,* **13**: 183–191.

T

Taylor, S.O., Lorimer, C., (2003). Loss of oak dominance in dry-mesic deciduous forests predicted by gap capture methods. *Plant Ecology*, **167**: 71–88.

Témoin, J.L., (2009). *Mise en place d'un réseau d'ilots de vieux bois en forêt domaniale de Rambouillet.* Rambouillet: 24p.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., (1994). Habitat destruction and the extinction debt. *Nature,* **371**: 65-66.

Timonen, J., Siitonen, J., Gustaffson, L., Kotiaho, J., Stockland, J.N., Sverdrup-Thygesson, A., Mökkönen, M., (2010). Woodland key habitats in northern Europe: concepts, inventory and protection. *Scandinavian Journal of Forest Research,* **25**: 309-324.

Tittler, R., Norton, M.N., Hannon, S.J., (2001). Residual tree retention ameliorates short-term effects of clear-cutting on some boreal songbirds. *Ecological Applications,* **11**: 1656-1666.

Tositti, A., (2004). *Ilots de vieux bois*. Tec. Rept. Institut d'Aménagement et d'Urbanisme de la région Ile-de-France.

Troll C., (1939). Luftbildplan und ökologische Bodemforschung. *Zeitschrift der Gesellschaft für Erdkunde zu Berlin*, 241-298.

Tscharntke, T., Steffan-Dewenter, I., Krues, A., Thies, C., (2002). Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research*, **17**: 229–239.

Turner, M.G., (2005). Landscape ecology: What Is the State of the Science? *Annual Review of Ecology and Evolution Systems,* **36**: 319–44.

U

Unruh, T.R., Chauvin, R.L., (1993). Elytral punctures: a rapid, reliable method for marking colorado potato beetle. *The Canadian Entomologist,* **125**: 55-63.

V

Vandekerkhove, K., de Keersmaeker, L., Menke, N., Meyer, P., Verschelde, P., (2009). When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. *Forest Ecology and Management,* **258**: 425–435.

Vera, F.W.M., (2000). *Grazing Ecology and Forest History*, CABI Publishing. 506p.

Victorsson, J., Jonsell, M., (2012). Ecological traps and habitat loss, stump extraction and its effects on saproxylic beetles. *Forest Ecology and Management,* **290**: 22–29.

Vignon, V., (2006). *Les trognes: Un habitat de substitution remarquable pour les coléoptères saproxyliques.* 1er Colloque Européen sur les trognes. Vendôme.

Virkkala, R., Alanko, T., Laine, T., Tiainen, J., (1993). Population contraction of the white-backed woodpecker Dendrocopos leucotos in Finland as a consequence of habitat alteration. *Biological Conservation,* **66**: 47-53.

Vodka, S., Konvicka, M., Cizek, L., (2009). Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *Journal of Insect Conservation*, **13**: 553–562.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., (2011). Influence of tree characteristics and forest management on tree microhabitats. *Biological Conservation*, **144**: 441–450.

W

Watson, S., (2003). *Dispersal and gene flow in Prostomis atkinsoni (Coleoptera)*. Melbourne, La Trobe University: 58p.

Werner, F. A. (2011). Reduced growth and survival of vascular epiphytes on isolated remnant trees in a recent tropical montane forest clear-cut. *Basic and Applied Ecology,* **12**: 172–181.

Whitehouse, N.J., Smith, D., (2004). 'Islands' in Holocene forests: Implications for Forest Openness, Landscape Clearance and 'Culture-Steppe' Species. *Environmental Archaeology*, **9**: 203–212.

Wilcox, B.A., Murphy, D.D., (1985). Conservation strategy: the effects of fragmentation on extinction. *American Naturalist,* **125**: 879-887.

Winter, S., Möller, G.C., (2008). Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management,* **255**: 1251–1261.

Wu, J., (2006). Landscape ecology, cross-disciplinarity, and sustainability science. *Landscape Ecology*, **21**: 1–4.

Y

Yu, W., Ji, Y., Emerson, B.C., Wang, X., Ye, C., Yang, C., Ding, Z., (2012). Biodiversity soup: metabarcoding of arthropods for rapid biodiversity assessment and biomonitoring. *Methods in Ecology and Evolution*, **3**: 613–623.

Z

Zolubas, P., Byers, J.A., (1995). Recapture of dispersing bark beetle Ips typographus L. (Col., Scolytidae) in pheromone-baited traps: regression models. *Journal of Applied Entomology,* **119**: 285-289.

Annexes

Table des annexes

Annexe 1: Travaux personnels sur les insectes saproxyliques.

Mes contributions à la connaissance de la biologie, taxinomie et répartition des espèces saproxyliques sont exposées ci-après. Elles consistent majoritairement en des publications naturalistes dans des revues soumises à un comité de lecture.

Publiées :

* **PARMAIN**, G. et SOLDATI, F. (2011). Taxonomie, écologie et répartition en France de *Melanopsacus grenieri* (Brisout de Barneville, 1867) (Coleoptera, Antrhibidae, Choraginae). *R.A.R.E*. XX (2).

* **Parmain**, G. ., Heiss, E., Brustel, H. (2012). New and additional faunal records of Aradidae from France, Spain and Morocco (Hemiptera, Heteroptera). *Nouvelle Revue d'Entomologie*, 28 (3/4), 243-256.

* Yves GOMY, Guilhem **PARMAIN** & Philippe MILLARAKIS (2012) *Teretrius (Neotepetrius) parasita* Marseul, 1862 (Coleoptera, Histeridae) : Espèce nouvelle pour la France continentale. *L'Entomologiste* **68** : 197-198.

* Fabien SOLDATI & Guilhem **PARMAIN (2013)** Découverte en France du mâle de *Megischina rosinae* (Seidlitz, 1896) et précisions sur l'écologie et la distribution de l'espèce dans les Pyrénées Orientales (Coleoptera, Tenebrionidea, Alleculinae). *R.A.R.E* **XXII** : 12-16.

* Christian COCQUEMPOT, Fabien SOLDATI et Guilhem **PARMAIN** *Xylotrechus stebbingi* (Gahan, 1906) nouveau pour le département de l'Aude (Coleoptera, Cerambycidae). *Rutilans.*

Soumises :

Par Julien DELNATTE, Guilhem **PARMAIN** & fabien SOLDATI (*submitted*) Nouvelles localités pour *Isidus moreli* Mulsant & Rey, 1874 (Coleoptera, Elateridae, Elaterinae) sur le littoral français. *Société Entomologique de France*.

En préparation :

Parmain et al. (in prep) *Phloiophilus edwarsii* Stephens, 1830 (Coleoptera, Phloiophilidae) nouveau pour les départements de la Charente, de l'Yonne du Loiret et de la Haute-Vienne.

Parmain et al (in prep) Distribution de *Pityophagus quercus* Reitter, 1877 (Coleoptera, Nitidulidae) en Europe et espèces de coléoptères saproxyliques remarquables associées.

Fleury, **Parmain** et al (in prep) Encore de nouvelles espèces détectées au domaine des Barres !

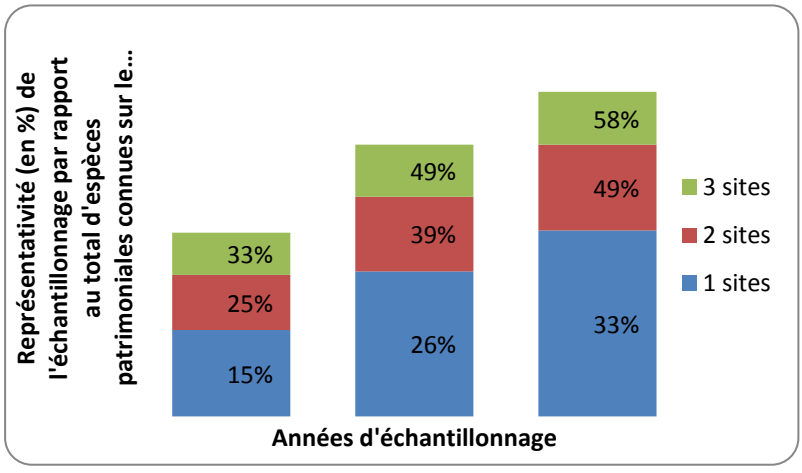
Annexe 2 : Pression d'échantillonnage et espèces patrimoniales en forêt de Tronçais

Les données qui ont permis cette exploration datent de 2010 et mériteraient d'être réévaluées. Elles sont issues d'une campagne de piégeage sur trois ans avec trois paires de pièges polytrap amorcés avec de l'éthanol. La durée d'échantillonnage et le nombre moyen de captures est identique pour les combinaisons 2 placettes x 1 an vs 1 placette x 2 ans et 3 placettes sur 2 ans vs 2 placettes sur 3 ans.

	1 placette		2 placettes		3 placettes	
Tronçais	Nombre moyen d'espèces bio-indicatrices contactées	Ecart type	Nombre moyen d'espèces bio indicatrices contactées	Ecart type	Nombre moyen d'espèces bio indicatrices contactées	Ecart type
1 an	11,44	3,5	18,77	3,6	24,33	4
2 ans	19,22	4,8	29,11	4,5	36	4
3 ans	24,66	6	36	4,3	43	NA

Nombre moyen d'espèces de coléoptères bio indicateurs contactés, en fonction du nombre de placettes et d'années d'échantillonnage.

On constate que l'ajout d'une année d'échantillonnage ou une paire de piège ont le même effet en termes de nombre d'espèces. Pour 3 placettes utilisées, les proportions passent de 33% pour une année d'échantillonnage à 58% pour trois années d'échantillonnage. L'utilisation de deux sites pendant 3 ans permet de contacter près de 50% des coléoptères bio-indicateurs connus à l'époque.



Evolution sur le site de Tronçais de la proportion moyenne du nombre d'espèces bio-indicatrices capturées par rapport au nombre total d'espèces bio-indicatrices connues, en fonction du nombre de placettes utilisées et du nombre d'années d'échantillonnages.

Annexe 3 : Projet de thèse initial

Sujet de thèse 2011-2014

« Trame de très vieux bois et biodiversité des coléoptères saproxyliques »

Présenté par Guillem Parmain

Sous la direction de Christophe Bouget

1. Contexte et enjeux

Le suivi et la protection des milieux forestiers en utilisant des indicateurs liés aux organismes saproxyliques (dépendant du bois mort [Speight 1989]) est une priorité pour l'Europe depuis 1988 (Comité des Ministres 1988a, 1988b). Cette question est encore actuellement au cœur des débats visant à intégrer les enjeux de biodiversité dans les politiques publiques, notamment dans l'aménagement du territoire.

1.1. Les IVB, instruments de gestion forestière en faveur de la biodiversité

Plusieurs mesures de gestion sont actuellement disponibles pour favoriser la conservation des cortèges saproxyliques forestiers (ONF 2005, 2009a, 2009b, 2009c ; Mouray et Touroult 2010). Parmi ces mesures, les îlots de vieux bois sont une mesure phare en France (ONF 2005, 2009b ; Rouveyrol 2009 ; Témoin 2009 ; Tositti 2004), mais aussi en Suisse (Lachat et Bütler 2007), et au Canada (Déry et Leblanc 2005). Il est à noter que des structures équivalentes existent dans les pays scandinaves (Timonen *et al*., 2010) et en Amérique (Tittler *et al*., 2001).

Le terme « Îlots de vieux bois » regroupe deux notions en France : les îlots de vieillissement et les îlots de sénescence:

Un îlot de vieillissement se définit comme un « *petit peuplement ayant dépassé les critères optimaux d'exploitabilité économique et qui bénéficie d'un cycle sylvicole prolongé pouvant aller jusqu'au double de ceux-ci. L'îlot de vieillissement peut faire l'objet d'interventions sylvicoles, les arbres du peuplement principal conservant leur fonction de production. Ces derniers sont récoltés à leur maturité et, en tout état de cause, avant dépréciation économique de la bille de pied. L'îlot de vieillissement bénéficie en outre d'une application exemplaire des mesures en faveur de la biodiversité (bois mort au sol, arbres morts, arbres à cavité). […]. Le recrutement d'îlots de vieillissement est examiné lors de l'élaboration de l'aménagement parmi les unités de gestion qui pourraient faire partie du groupe de régénération et leur maintien est examiné à chaque révision d'aménagement forestier* » (ONF 2009b).

L'îlot de sénescence se définit comme un « *petit peuplement laissé en évolution libre sans intervention culturale et conservé jusqu'à son terme physique, c'est-à-dire jusqu'à l'effondrement des arbres. Les îlots de sénescence sont composés d'arbres de faible valeur économique et qui présentent une valeur biologique particulière (gros bois à cavité, vieux bois sénescents…). Les îlots de sénescence sont donc préférentiellement recrutés dans des peuplements de qualité technologique moyenne à médiocre, des peuplements peu accessibles, des séries boisées d'intérêt écologique… Pour des raisons de sécurité et de responsabilité, ils sont choisis hors des lieux fréquentés par le public.* » (ONF 2009b).

En fonction de leur surface et de leur capacité à générer du bois mort, les îlots de sénescence peuvent être permanents ou itinérants (Lachat et Bütler 2007). La taille moyenne d'un îlot de vieux bois est actuellement d'environ 1ha (Tositti 2005), surface assurant la présence de bois mort au cours du temps (Lachat et Bütler 2007).

D'un point de vue biologique, les îlots de sénescence sont préférables aux îlots de vieillissement (Lachat et Bütler 2007). Le cycle de vie complet des sujets âgés du peuplement est mené à terme. Les populations d'organismes saproxyliques de haut niveau trophique peuvent accomplir de nombreux cycles vitaux complets. Dans les îlots de vieillissement, les populations d'organismes saproxyliques de moyen et haut niveau trophique qui s'installent sont fortement défavorisées voire détruites par l'exploitation de ces îlots.

Les taux d'îlots de vieux bois recommandés par l'ONF en forêt publique sont variables en fonction de la surface de la forêt ainsi que de la présence ou non de RB. Les différents objectifs son récapitulés dans le tableau 1.

	Surface forestière			Cas particuliers	
	moins de 300ha	300ha	plus de 300 ha	Zones à forts enjeux de préservation	Zones de montagne
Ilot de vieillissement	Pas de seuil minimal	1%	2%	Entre 2% et 5%	De 2% à 5% ou plus
Ilot de sénescence			1%	Entre 1% et 3%	De 1% à 3% ou plus
Nombre d'aménagements pour arriver à l'objectif	Pas de durée définie	3 (entre 30 et 60 ans)		3 ou moins (60 ans au plus)	

Tableau 1 : récapitulatif des surfaces et durées de mises en place d'ilot de vieux bois en forêts publiques (ONF 2009a).

En forêt privée, aucune restriction n'est imposée. La conservation d'arbres-habitat ou la mise en place d'îlots de vieux bois sont laissés à la libre appréciation du propriétaire. Pour encourager la création d'ilots de vieux bois en forêt privée, des indemnisations sont proposées aux propriétaires dans des cas particuliers. Ainsi, le propriétaire d'une zone forestière inclue dans un site Natura2000 peut demander à être indemnisé pour la mise en place d'ilots de vieux bois sur sa propriété (ONF 2005). Des mesures compensatoires similaires sont également mises en place en Suisse (Lachat et Bütler 2007).

L'arbre-habitat est un élément qui vient renfoncer le réseau créé par les îlots de vieux bois au sein de la forêt. Il s'agit généralement d'un arbre vivant porteur de structures favorables à la biodiversité (cavités hautes, polypores, écorces déhiscentes…). Il peut également se présenter sous la forme d'un vieil arbre ou d'un très gros arbre de l'essence objectif ou des essences d'accompagnement (ONF 2009a). Un cas particulier de l'arbre-habitat est l'arbre mort. Certains auteurs considèrent cet arbre comme du bois mort sur pied et ne l'intègrent pas en tant qu'arbre-habitat (Lachat et Bütler 2007). Actuellement, l'ONF préconise le maintien d'une moyenne minimale de 3 arbres-habitat par hectare (ONF 2009a). Lachat et Bütler (2007) estiment pour leur part entre 8 et 12 le nombre minimal d'arbres-habitat à conserver par hectare dans les forêts Suisses.

Les IVB et l'arbre-habitat forment un réseau intra forestier avec les réserves forestières. On dénombre actuellement 205 Réserves Biologiques (RB) de tous types (RBI, RBD, RBM, RBF) en France dont 188 pour le seul territoire métropolitain (ONF Données internes). Elles constituent le maillon principal de la TTVB. La continuité temporelle de bois mort et la diversité de l'ensemble des phases de la sylvigenèse y est assurée, du moment que leur taille atteint au moins la centaine d'hectares (Lachat et Bütler 2007). Leur grande surface et leur stabilité temporelle comparée à celle des îlots de vieux bois leur confèrent un rôle de refuge important pour la biodiversité forestière (Löhmus et Löhmus 2010 ; Laita *et al*., 2010).

1.2. La Trame de très vieux bois (TTVB)

La fragmentation des habitats est aujourd'hui considéré comme une des causes majeures de l'érosion de la biodiversité (Ehrlich 1988 ; Wilcox et Murphy 1985). Le risque d'extinction local des espèces se maintenant sur de faibles surface est élevé (Gilg 2005). Lorsque ces surfaces augmentent, leur fréquence augmente et leur probabilité d'extinction diminue (Sahlin et Schroeder 2010). En réponse à ce phénomène, rétablir et/ou renforcer les liens entre les différentes parties d'un habitat en vue d'augmenter sa connectivité est une stratégie d'action. L'augmentation de la connectivité du milieu permet également d'augmenter virtuellement sa surface. C'est le principe du Réseau écologique paneuropéen (Conseil de l'Europe 2003) et de la Trame Verte et Bleue, issue du Grenelle de l'Environnement.

La constitution de la Trame Verte et Bleue implique de nombreux éléments, dont les forêts constituent un maillon essentiel. Les différents constituants de la diversité structurelle des forêts sont autant de variables permettant la constitution de réseaux internes à la Trame Verte et Bleue. Le cas particulier du compartiment écologique des "habitats saproxyliques" permet de discerner une structure intrinsèque à la Trame Verte et Bleue, la **Trame de Très Vieux Bois** (TTVB). Elle est constituée d'éléments répartis sur l'ensemble du territoire national français, pouvant être forestiers ou non forestiers.

- La place des IVB dans la TTVB

Les IVB permettent d'assurer la présence de vieux bois dans les forêts et plus précisément dans les zones soumises à une exploitation intense. Les taux de bois mort en zone exploitée sont généralement faibles comparativement à ceux des forêts non exploitées ou anciennement exploitées (Penttilä *et al*., 2004 ; Siitonen *et al*., 2000). Les différentes classes de bois mort (petit bois frais, gros

bois debout ou au sol, houppiers morts...) constituent autant d'habitats pour les organismes saproxyliques et n'y sont généralement pas représentées (Michel et Winter 2009). Dans ces conditions, l'habitat des espèces saproxyliques disparaît, pouvant entraîner la disparition locale de certaines d'entre elles (Hammond *et al*., 2004).

Ces différents micro-habitats ne doivent pas être trop éloignés les uns des autres pour permettre à la faune saproxylique de les coloniser.

Pour cela, les IVB sont généralement espacés les uns des autres par de faibles distances, de l'ordre de 1km en moyenne (Tositti et Cauchetier 2005). Cette répartition spatiale consolide le rôle d'élément de réseau des IVB. Ils œuvrent à deux échelles: au niveau local en assurant un réseau de bois mort au sein du site forestier, mais également au niveau national, en offrant un point "relais" pour la TTVB.

- Autres éléments forestiers de la TTVB

D'autres structures forestières participent à la structuration de la TTVB. Leur contribution relative à la connectivité de la TTVB ainsi que leur capacité à fournir un habitat propice aux organismes saproxyliques est mal connu (Degron et Gallemant 1999 ; Témoin 2009). Ces caractéristiques sont estimées dans le tableau 2.

		Eléments forestiers de la TTVB				
		Arbre-habitat	Ilots de vieux bois		Réserve biologique	Ripisylves
			îlots de vieillissement	îlots de sénescence		
Rôle dans la connectivité des habitats saproxyliques	Intra forestière	+++	++	+++	+	++
	Inter forestière	---	--	--	-	++
Micro-habitats saproxyliques (capacité d'accueil)		+	++ (selon âge)	+++ (selon âge)	+++ (selon âge)	++ (selon âge et taille)
Milieu refuge ?		+	+	++	+++	+++
Stabilité temporelle ?		-	--	-	+++	++

Tableau 2 : Eléments forestiers constitutifs de la TTVB: caractéristiques fonctionnelles. Légende: --- nul, -- négligeable, - peu important, + faible, ++ important, +++ essentiel.

Le cas particulier des ripisylves est à expliciter. Selon Piégay *et al*. (2003), la ripisylve est "*la forêt riveraine d'un cours d'eau, elle peut correspondre à un corridor très large comme à un liseret étroit et se compose d'entités floristiques variées, à bois durs ou à bois tendres* [...]". Cette définition ne saurait être en accord avec celle de l'IFN, puisqu'une forêt doit être large d'au moins 20 mètres (IFN 2011). Au Québec, le terme ripisylve est remplacé par le terme de "bandes riveraines" qui englobe les notions de forêt alluviale et d'alignement boisés de bord de cours d'eau ou de lacs (Gagnon et Gangbazo 2007). C'est dans ce sens que nous utilisons le terme de ripisylve.

La dynamique des bois morts et de l'apparition de micro-habitats favorables aux organismes saproxyliques est accélérée dans les ripisylves (Bouget 2008), ce qui en fait un excellent milieu refuge pour les organismes saproxyliques de haut niveau trophique. De plus, certaines espèces d'insectes saproxyliques se retrouvent exclusivement en bordure de cours ou dans les milieux humides (Leseigneur 1972 ; Bouget 2008).

- Eléments non forestiers de la TTVB

La TTVB ne se limite pas aux structures forestières. Des éléments boisés tels que les parcs urbains ou encore les bosquets (IFN 2001), les arbres isolés sont autant de constituants de la TTVB. Ils sont d'origine variable (lambeaux d'anciennes forêts, arbres repères...) mais ont tous une valeur de refuge importante pour les espèces saproxyliques (Borges *et al*., 2005 ; Borges *et al*., 2006 ; Jonsell 2004 ; Meriguet et Zagatti 2004 ; Ohsawa 2007 ; Vignon 2006).

Nous utilisons les termes de bosquets et de haies de façon plus large que l'IFN (2011). Dans notre cas, le terme de bosquet englobe également les parcs urbains, les ilots boisés dans une matrice non forestière (urbaine, agricole)… Chaque un de ces éléments a une surface comprise entre 0.5ha et 5ha.

Nous considérons qu'en plus de leur définition (IFN 2011), les haies englobent les alignements d'arbres et la partie des bocages ne correspondant pas à des arbres isolés (Dubois 2009).

		Eléments non forestiers de la TTVB		
		Arbres isolés	Haies	Bosquet
Connectivité forestière	Intra forestière	---	---	---
	Inter forestière	+	+	+

Micro habitats saproxyliques	++	++	+
Milieu refuge	+++	++	++
Stabilité temporelle	+	++	+++

Tableau 3 : Eléments non forestiers constitutifs de la TTVB: caractéristiques fonctionnelles. Légende: -- - nul, -- négligeable, - peu important, + faible, ++ important, +++ essentiel.

Peu d'études se sont focalisées sur la capacité d'accueil des différents éléments non forestiers de la TTVB vis-à-vis des coléoptères saproxyliques. La plupart des études existantes à travers le monde concernent les fourmis (Gove *et al*., 2009 ; Dunn 2000), les chauves souris (Lumsden et Bennett 2005) ou encore les plantes épiphytes (Werner 2010). En Europe, aucune étude n'a encore comparé la contribution respective de chaque élément non forestier de la TTVB vis-à-vis des coléoptères saproxyliques. Des études au cas par cas assimilables à des explorations faunistiques ont été menées pour certains de ces éléments (Borges *et al*., 2005 ; Borges *et al*., 2006 ; Carpaneto et Mazziotta 2010 ; Dubois 2009 ; Jonsell 2004 ; Meriguet et Zagatti 2004 ; Ohsawa 2007 ; Vignon 2006).

La plupart de ces éléments sont en régression depuis 1960 (Boureau *et al*., 2005 ; Pointereau et Coulon 2006). Le rythme de disparition des haies était élevé entre 1960 et 1980 (45.000 km/an) puis a diminué entre 1980 et 1990 (15.000km/an) et s'est stabilisé depuis (Pointereau et Coulon 2006). On observe également un accroissement de l'âge des arbres constitutifs des haies alors que leur linéaire diminue (Pointereau 2001). Ceci pose la question de leur renouvellement et de la survie des espèces d'insectes saproxyliques qui s'y sont réfugiées.

1.3. Vieillissement et trame d'habitat, contexte scientifique

1.3.1. Gradient de vieillissement des peuplements forestiers

Pour différencier les termes Vieux et Ancien, Robert (1977) nous donne les définitions suivantes : (i) Ancien : « *Qui existe depuis longtemps, qui date d'une époque bien antérieure* », (ii) Vieux : « *Qui a vécu longtemps ; qui est dans la vieillesse ou qui paraît l'être* ».

Dans le cas particulier des forêts ces deux termes traduisent deux réalités différentes. Une forêt, à la différence d'un être vivant n'a pas de durée de vie théorique maximale. Son existence est déterminée -hors action anthropique- par des phénomènes naturels de grande échelle telles les glaciations (Demesure et Musch 2001). Ainsi, après la dernière glaciation en Europe, 80% de sa surface était recouverte de forêt (Gilg 2005). Ces surfaces reliques, que l'on peut appeler des forêts

anciennes, sont actuellement estimées à moins de 1% de la surface totale des forêts en Europe (Gilg 2005).

L'identification des forêts anciennes en France est difficile. Bien souvent les archives concernant la gestion des forêts ne remontent pas au-delà des cartes de Cassini (XVII^{è} au XIX^{è}). L'atlas de Trudaine datant de 1745-1780 et cartographiant les routes royales françaises et leurs alentours peuvent apporter un complément d'information ponctuel. Cependant, même les forêts présentes sur ces cartes ont pu connaitre des déboisements totaux puis être replantées ou régénérées. Il faut pour cela les confronter avec les cartes d'état major (XIX^{è} siècle), plus précises (voir Doupouey *et al*., 2007).

Ainsi, on peut globalement considérer comme forêt ancienne les forêts présentes sur l'ensemble de ces cartes et existant encore de nos jours. Toutefois, de nombreuses nuances sont à apporter à cette définition.

Par opposition, une forêt qui ne répond pas à la définition de forêt ancienne sera considérée comme récente (Doupouey *et al*., 2007).

Les arbres au sein d'une forêt ont une durée de vie limitée allant de 40 à plus de 500 ans (Lanier 1986). A l'échelle de la forêt, il n'est donc pas pertinent de parler d'arbre ancien. Il est préférable d'employer le terme d'arbre vieux. En fonction des essences, un arbre de même âge peut être jeune ou vieux.

Il est important de noter que le terme « d'arbre vieux » n'a pas la même signification pour les forestiers que pour les naturalistes. Le forestier va considérer un arbre comme vieux un fois qu'il a dépassé son âge d'exploitabilité. Or, pour le naturaliste, un arbre vieux est un arbre qui entame sa phase de sénescence. En fonction des essences, l'écart qu'il peut y avoir entre un arbre vieux au sens forestier et un arbre vieux au sens du naturaliste varie entre quelque dizaines d'années et plusieurs siècles (Lanier 1986) ! Il y a donc une incompréhension potentielle entre les naturalistes et les forestiers quand à la sélection des vieux arbres à conserver. Dans la suite du document, le terme « vieux » sera employé au sens du naturaliste.

En tenant compte de ces considérations, il est possible de définir 4 catégories principales de forêts :

- Les forêts anciennes avec de vieux peuplements
- Les forêts anciennes avec de jeunes peuplements

- Les forêts récentes avec de vieux peuplements
- Les forêts récentes avec de jeunes peuplements

Dans tous ces cas de figures, les forêts peuvent avoir été ou être exploitées.

- Old-growth, Green tree retention et Woodland key habitat

Le terme « Old-growth forest » (OGF) désigne des forêts à vieux peuplements. Cette dénomination ne véhicule pas forcément une notion de continuité forestière, contrairement au terme anglo-saxon de « ancient woodland » (Kirby *et al*., 1995). Des forêts récentes peuvent être des OGF. En fonction des pays, les seuils d'âge appliqués aux différent gradients de vieillissement des forêts ne sont pas les mêmes (tableau 4).

	Classes de vieillissement						
Auteurs (Pays)	**Clearcut**	**Young**	**Middle-age**	**Mature**	**Overmature managed**	**Old**	**Old-growth**
Michel et Winter 2009 ; Zenner 2000 (USA)	0-1 an	20-50 ans	51-80 ans	81-150 ans		121-250 ans	> 250 ans
Siitonen *et al*., 2000 (Finlande)				95-118 ans	124-145 ans		129-198 ans

Tableau 4 : Comparaison des classes d'âges associées à différents niveaux de vieillissement de la forêt entre les USA et la Finlande.

Tout comme les forêts anciennes à vieux peuplements, les OGF présentent de nombreux micro-habitats favorables à la faune saproxylique des forêts (Gilg 2005). Dans les forêts exploitées, de telles structures se font rares. Un des moyens pour maintenir un niveau suffisant de micro-habitats favorables à la biodiversité saproxylique est de soustraire des portions de forêt à l'exploitation. A terme, ces aires sont prévues pour posséder les caractéristiques des OGF. En France, les îlots de vieux bois ont été créés à cet effet (ONF 2009a, 2009b). En Amérique et dans les pays scandinaves, une structure similaire existe, les « green tree retention »(GTR) (Addison 2007; Aubry *et al*., 1999 ; Aubry *et al*., 2004 ; Aubry *et al*., 2009 ; Gustafsson *et al*., 2010 ; Hautala *et al*., 2004 ; Hautala *et al*., 2009 ; Hazel et Gustafsson 1999 ; Hedenas et Hedström 2007 ; Hyvärinen *et al*., 2009 ; Jairus *et al*., 2009 ; Löhmus et Löhmus 2010 ; Maguire *et al*., 2007 ; Martikainen *et al*., 2006 ; Matveinen-Huju *et al*., 2006 ; Perhans *et al*., 2009 ; Pitkänen *et al*., 2005 ; Rose et Muir 1997 ; Rosenvald et Löhmus 2008 ;

Svedrup-Thygesson et Ims 2002 ; Svedrup-Thygesson et Birkemoe 2009 ; Tittler *et al*., 2001 ; Vanha-Majamaa et Jalonen 2001 ; Wagner *et al*., 2010 ; Work *et al*., 2010). La lecture des articles cités permet d'effectuer un bilan sur ce que sont les GTR. Contrairement aux îlots de vieux bois en France, les GTR sont très variables. Ils n'ont pas de taille minimale puisque parfois, seuls quelques arbres sont conservés, dispersés ou groupés au sein de la zone exploitée. Les études portant sur la taille minimale des GTR sont en accord pour dire qu'un hectare est la taille minimale des GTR pour qu'ils puissent assurer leurs fonctions, mais que des tailles supérieures seraient préférables. Plusieurs auteurs soulignent également l'importance de conserver sur la même parcelle des GTR dispersés et groupés. Dans l'ensemble, les GTR permettent le maintien à court terme des espèces sensibles à la fragmentation forestière. Le rôle des GTR ne se limite pas seulement à la préservation ponctuelle des espèces sensibles à la fragmentation forestière, mais s'inscrit dans une logique de réseau en lien étroit avec les réserves forestières.

Une structure supplémentaire semble spécifique aux pays Scandinaves, les « woodland key habitat »(WKH) (Andersson et Kriukelis 2002 ; Aune *et al*., 2005 ; Berg *et al*., 2002 ; Ek et Bermanis 2004 ; Ericsson *et al*., 2005 ; Gjerde *et al*., 2004 ; Götmark 2009 ; Gustafsson *et al*., 1999 ; Gustafsson 2000 ; Hottola et Siitonen 2008 ; Johansson et Gustafsson 2001 ; Laita *et al*., 2010 ; Siitonen *et al*., 2009 ; Sippola *et al*., 2005 ; Timonen *et al*., 2010). Timonen *et al* (2010) ont fait un récent travail de synthèse sur les WKH en Europe du nord. Il en ressort que la définition même de WKH est différente en fonction des pays. Cependant, dans tout les pays, les WKH sont présentés comme des zones particulièrement importantes pour la biodiversité forestière et abritent ou sont supposés abriter des espèces menacées. Ils sont de taille variable, allant de 0,4 à 4,6 ha et ne sont pas répartis de manière égale sur les territoires. Ils assurent avec les réserves et les GTR un réseau d'habitats favorables aux espèces sensibles à l'exploitation forestière et à la fragmentation des habitats.

L'application de ces mesures de conservation est récente, elle date d'environ 20 ans (Timonen *et al*., 2010). Nous n'avons donc pas encore assez de recul pour comparer de manière pertinente les effets du vieillissement des peuplements de ces structures sur la biodiversité saproxylique. Cependant, les résultats préliminaires indiquent que l'impact des GTR et des WKH est plutôt positif pour la biodiversité saproxylique (Hazel et Gustafsson 1999 ; Hottola et Siitonen 2008 ; Hyvärinen *et al*., 2009 ; Jairus *et al*., 2009 ; Sippola *et al*., 2005), mais sans plus de précisions.

1.3.2. La TTVB : écologie du paysage et biodiversité saproxylique

La TTVB est composée de nombreux éléments (détaillés paragraphe 1.2). Ils ne sont pas repartis de manière homogène sur l'ensemble du territoire national. Leur connectivité à des échelles spatiales et temporelles n'a pas été et n'est pas encore forcément assurée. La fragmentation des habitats forestiers actuels est le résultat d'une exploitation des ressources et des surfaces forestières depuis plusieurs millénaires (Bouget et Brustel 2010). Au cours de son histoire, la surface forestière française à évolué, en passant par de très faibles surfaces (16% du territoire national au milieu du 19^{e} siècle). Actuellement, l'IFN estime à 28,6% la surface de forêt sur le territoire national (IFN 2008), soit environ le double de la surface minimale ayant existé aux alentours de 1850. Actuellement, un peu plus de la moitié de la surface forestière française est constituée de plantations et de recolonisation naturelle après déprise (Cinotti 1996).

Cette configuration du paysage est synonyme de perte de biodiversité liée à la fragmentation spatiale et temporelle des habitats (Bouget et Brustel 2010). Des mises en garde à ce sujet ont été émises par d'autres auteurs depuis longtemps déjà (Norse *et al.*, 1986).

En général, plus le micro-habitat d'une espèce est durable dans le temps, plus les capacités de dispersion de l'espèce sont faibles (Dubois 2009).

La plupart des coléoptères saproxyliques primaires (Brustel 2004) est moins affectée par la fragmentation des forêts. Ils possèdent de fortes capacités de dispersion leur permettant de rejoindre des habitats distants les uns des autres. C'est par exemple le cas pour certaines espèces de Scolytidés se développant sur du bois fraîchement mort. Ils sont capables de parcourir des distances de plusieurs kilomètres pour trouver un habitat favorable (Williams et Robertson 2008).

D'autres en revanche ne possèdent pas de telles capacités de dispersion. Certaines espèces telle *Osmoderma eremita* qui occupe les cavités hautes de arbres, s'organisent en systèmes de métapopulations (Ranius et Hedin 2001). La fréquence et la taille des populations diminuent avec l'augmentation de l'isolement de son habitat (Carpanetto *et al.*, 2010). Les capacités de dispersion de cette espèce sont faibles, la distance maximale de déplacement observée varie entre 180m (Hedin *et al.*, 2008) et 700m (Dubois 2009), bien qu'en conditions de laboratoire, la distance cumulée parcourue par un individu atteint 2360m (Dubois 2009). De plus les modèles mathématiques prévoient que peu d'individus (15%) dispersent au sein de chaque population (Ranius et Hedin 2001).

D'autres espèces s'organisent suivant le même modèle (Schroeder *et al.*, 2007; Svedrup-Thygeson et Midtgaard 1998) mais dans d'autres types d'habitats de haut niveau trophique (Galindo-Cardonna *et*

al., 2007 ; Jonsell *et al*., 1999 ; Jonsell *et al*., 2003) tels les polypores ou les gros bois en état de décomposition avancé.

1.3.3. Les IVB : vieillissement des peuplements et biodiversité saproxylique

Les différentes intensités d'exploitation forestière (non exploitation / coupe à blanc fréquente) produisent une grande variété de paysages, aux âges et aux structurations variées (Michel et Winter 2009). Ces différentes structurations sont plus ou moins favorables aux organismes saproxyliques. Plus les paysages –et les peuplements- issus de l'exploitation forestière sont jeunes, plus leur volume de bois mort est faible (Siitonen *et al*., 2000 ; Moorman *et al*., 1999). Les forêts à caractère naturel (Old-growth forest) sont celles qui présentent les volumes de bois mort les plus importants ainsi que les arbres de plus grand diamètre (Nilsson *et al*., 2003 ; Siitonen *et al*., 2000 ; Zenner 2004). Le constat est le même concernant les micro-habitats favorables aux organismes saproxyliques (Fan *et al*., 2003). La diversité des micro-habitats diminue d'autant plus que l'exploitation forestière est intense (Michel et Winter 2009) et que les peuplements qui en résultent sont jeunes.

Les organismes saproxyliques sont sensibles aux niveaux de bois mort et à la disponibilité en micro-habitats du milieu forestier. Ces deux composantes sont corrélées négativement à l'intensité de l'exploitation forestière. On aboutit donc dans les forêts intensivement exploitées à une dominance des jeunes peuplements. Il en résulte un milieu défavorable aux espèces saproxyliques tributaires d'arbres vivants de fort diamètre, de forts volumes de bois mort, et de micro-habitats spécifiques aux forêts à vieux peuplements (forêts à caractère naturel). Ces observations sont vérifiées dans plusieurs pays pour les lichens (Boudreault *et al*., 2002 ; Moning et Müler 2009 ; Nascimbene *et al*., 2010), les bryophytes (Boudreault *et al*., 2002), les mollusques (Moning et Müler 2009), les coléoptères (Grove 2002 ; Hammond *et al*., 2004 ; Martikainen *et al*., 2000 ; Similä *et al*., 2002a ; Similä *et al*., 2002b ; Stenbacka *et al*., 2010), des parasites de coléoptères saproxyliques (Hilszczański *et al*., 2005), les oiseaux (Moning et Müler 2009) et les polypores (Pentilliä *et al*., 2004). L'impact fortement positif de vieux arbres dans des parcelles exploitées sur la présence de chauves souris a également été mis en évidence (Mazurek et Zielinski 2004).

Les cortèges de coléoptères saproxyliques et de polypores sont significativement différents entre les forêts fortement exploitées à jeunes peuplements et les forêts à caractère naturel (Pentillia *et al*., 2004 ; Stenbacka *et al*., 2010). De plus, les espèces présentes sur les listes rouges sont plus fréquemment retrouvées dans les forêts à caractère naturel que dans les forêts exploitées, pour les

coléoptères (Similä *et al*., 2002a) pour les polypores (Penttilä *et al*., 2004) et pour les lichens (Nascimbene *et al*., 2010).

2. Objectifs, questions et hypothèses de travail

Il s'agit de comprendre le rôle des peuplements sur-matures tels les îlots de vieux bois vis à vis des cortèges de coléoptères saproxyliques. Il s'agit plus largement de comprendre le fonctionnement des peuplements sur-matures en tenant compte de leur environnement à différentes échelles spatiales et temporelles.

De nombreuses études concernant la fragmentation des habitats ont été réalisées dans le cas de groupes taxinomiques ou d'espèces particulières (Haddad 2000 ; Telleria *et al*., 2003 ; Wolff *et al*., 1997), mais aucune ne s'est encore intéressé à la fois aux relations entre cortège de coléoptères saproxyliques, fragmentation de la continuité forestière, et ancienneté du milieu. Hunter (2002) déplore le manque d'études menées sur les insectes et leurs relations vis-à-vis de la connectivité des milieux fragmentés.

Le but de cette étude est d'*évaluer le rôle des différents composants forestiers et non forestiers de la trame de très vieux bois (TTVB) en tant qu'éléments de conservation des cortèges de coléoptères saproxyliques sur un gradient de vieillissement et d'ancienneté des peuplements.*

Nous partons des constats de la littérature scientifique pour appuyer nos axes de recherches :

La haute connectivité des habitats permet la conservation efficace d'espèces menacées (Carpanetto *et al*., 2010). Certains éléments de la TTVB sont connus pour être un refuge important pour les espèces saproxyliques (Vignon 2006). Cependant, le cortège d'espèces saproxyliques pourrait être diminué par rapport au milieu forestier.

Les cortèges de coléoptères saproxyliques sont différents en fonction de l'âge des peuplements. Les espèces dépendant de hauts niveaux de dégradation du bois sont le plus souvent des espèces à forte valeur patrimoniale et aux enjeux de conservation particuliers (Brustel 2004).

L'identification des forêts anciennes en France est délicate (Dupouey *et al*., 2007). Certaines espèces ne se retrouvent que dans les milieux ayant conservé une continuité forestière importante (Siitonen et Saaristo 2000).

Dès lors, trois questions principales émergent :

- Q1=Dans les paysages avec une densité de trame de très vieux bois contrastée (trame de très vieux bois connectée vs déconnectée), quelle est la contribution respective des éléments de la trame de très vieux bois à la biodiversité des coléoptères saproxyliques ?
- Q2=Quelle est la dynamique de la biodiversité des coléoptères saproxyliques sur un gradient de vieillissement des peuplements forestiers ?
- Q3=Quel est l'impact de l'ancienneté forestière sur les cortèges de coléoptères saproxyliques ?

3. Méthodes

3.1. Plans d'échantillonnage

3.1.1. Typologie de paysages avec densité de trame de très vieux bois contrastée (TTVB connectée vs déconnectée)

Pour limiter les facteurs confondants et ne pas disperser l'effort d'échantillonnage, nous restreindrons nos sites d'étude aux chênaies de plaine.

Propositions de forêts d'étude	**Gradient de vieillissement**		
	Matur (100-250(	**Vieux (250 et +(**	**Total pièges**
Tronçais			

Fontainebleau			
Compiègne			
Clos de Bercé			
Cadarache			
? Citeaux ?			
? Sare ?			
? Maures ?			
Total pièges			**≤ 100**

Tableau 5 : Etude de la relation entre vieillissement des peuplements et biodiversité saproxylique.

Echelle	**Forestier**	**Elément**	**Paysage 1**	**Paysage 2**	**Paysage 3**	**Paysage 4**	**Total**
Arbre	+	Arbre-habitat					
Groupe d'arbres	+	Vieux peuplement					
Groupe d'arbres	+/-	Ripisylve					
Arbre	-	Vieil arbre isolé					
Groupe d'arbres	-	Haies					
Groupe d'arbres	-	Bosquet					
		Total					**≤ 100**

Tableau 6 : Evaluation de la contribution des différents éléments de la TTVB au maintien de la biodiversité saproxylique.

La question de l'intégration de témoins (arbres non-habitat et peuplement forestier non vieux) reste posée.

Dans tous les cas de figure, un historique rapide des milieux échantillonnés devra être réalisé. Le but est de discerner les zones ayant eu de grandes surfaces ou une grande connectivité il y a peu de

temps pour se prémunir ou intégrer un effet rémanence des populations d'insectes saproxyliques. Les populations d'insectes saproxyliques peuvent mettre du temps à s'éteindre localement et n'indiquent pas forcément que l'habitat est propice au maintien de l'espèce (Gilg 2005). Ce phénomène porte le nom « d'extinction debt » (Baldi et Vörös 2006, Hanski et Ovaskainen 2002, Tilman *et al*., 1994, Triantis *et al*., 2010).

3.2. Etude de la capacité d'accueil de l'entomofaune saproxylique

3.2.1. Caractérisation de l'environnement

- Paysage

Une fiche descriptive des différents sites d'étude que nous souhaitons explorer dans le tableau5 est en cours d'élaboration. Pour aider à localiser ces sites en France, la contribution des réseaux naturalistes de l'ONF sera sollicitée.

Critères de sélection proposés:

- essence dominante des vieux arbres = Chêne
- peuplement d'arbres (pas d'alignement)
- surface minimale = 3ha
- classe d'âge minimale des vieux arbres = 250 ans
- privé ou public
- vieux arbres aujourd'hui en forêt et avec passé forestier ou agroforestier

La sélection de sites issue de l'enquête sera validée par une exploration de terrain de chaque un d'entre eux. L'implication de ou des agents locaux doit permettre une localisation efficace des éléments de la TTVB au sein des sites étudiés.

Une fiche descriptive des différents éléments du paysage que nous souhaitons traiter dans le tableau6 est en cours d'élaboration. Pour aider à localiser ces paysages ateliers en France, la contribution des réseaux naturalistes de l'ONF sera également sollicitée.

Critères de sélection communs :

- maximum d'éléments de la TTVB sur une faible surface
- taille de la fenêtre de paysage en fonction de l'existant : 30x30km

Critères spécifiques :

- Haies :
    - Longueur > 25m
    - Hauteur des arbres > 5m
    - Distance entre les arbres > 5m
- Arbres isolés :
    - Vieux
    - Distance à l'arbre le plus proche > 50m
- Bosquets :
    - Surface entre 0,5 et 5ha

Sur l'ensemble des paysages choisis, un certain nombre de caractéristiques seront à renseigner pour permettre la comparaison des sites entre eux et de fixer d'éventuels biais :

- taux de boisement ?
- taux d'urbanisation ?
- latitude
- histoire (difficile de trouver un descripteur simple pour stratifier…)
- connectivité de la TTVB (densité d'éléments de vieux bois sur la surface de paysage)
- autres…

Exemple de sites (Propositions) :

- Ripisylve : Aube / Champagne (Peuplier Aulne Chêne Bouleau)
- Bosquets isolés : Aube / Champagne (Pins sylvestre et Bouleau)
- Haies : Limousin (études déjà faites sur compositions, localisations et connectivité, Chêne)

De nombreux paramètres sont à contrôler pour éviter un maximum d'effets confondants comme par exemple l'effet 'essence' (différente en ripisylve par ex.) entre les paysages sélectionnés.

D'autres questions se posent, comme par exemple la possibilité de conserver du matériel dans un état suffisamment bon pour des analyses génétiques. La question de l'étude de traits morphométriques des espèces communes aux différents éléments de la TTVB est également envisagée telle la taille, mesures alaires… (Gibb *et al*., 2006).

D'un point de vue pratique, piéger dans les zones privées peut poser un problème de délai d'obtention des autorisations des propriétaires. Pire encore, un refus pur et simple n'est pas à exclure.

- Peuplement et micro-habitats

Pour un insecte saproxylique, un micro-habitat peut être réduit à quelques dm^3 de bois (Brustel 2004). Une description de l'environnement immédiat du piège doit être envisagée -en plus d'une description à une échelle plus large de chaque site- pour mieux comprendre ces relations. Actuellement, des pièges séparés par une distance minimale de l'ordre de 20-25m peuvent être considérées comme indépendants (Bouget et Nageleisen 2009 ; Fan *et al.*, 2007 ; Giblin-Davis *et al.*, 1994). Une distance de 30m semble pertinente pour définir un diamètre de la placette à décrire autour de chaque piège afin de caractériser son environnement immédiat.

3.2.2. Caractérisation de l'entomofaune

Un travail de synthèse sur l'étude des insectes en forêt a été récemment produit par le groupe de travail Inv.Ent.For (Bouget et Nageleisen 2009). La pertinence et la rigueur scientifique de ce travail ont été validées par le Muséum d'histoire naturelle, l'ONF, l'OPIE, le CEMAGREF, Réserves Naturelles de France, l'Ecole d'Ingénieurs de PURPAN et le Ministère de l'Alimentation de l'Agriculture et de la Pêche (Département de la Santé des Forêts). Ce document a servi de base pour l'élaboration de notre protocole d'échantillonnage.

Les coléoptères sont utilisés dans de nombreuses études pour discuter des différences entre forêts exploitées et non exploitées mais aussi entre milieu fragmenté et non fragmenté (Tableau 7). La plupart du temps, ces coléoptères appartiennent au groupe fonctionnel des saproxyliques. C'est un groupe particulièrement étudié car relativement bien connu, facilement échantillonnable et représentant 20% des espèces saproxyliques forestières (Bouget 2008).

Perturbation anthropique de la forêt	Gibb *et al.*, 2006a ; Gibb *et al.*, 2006b ; Laaksonen *et al.*, 2008 ; MacGeoch *et al.*, 2007 ; Schroeder *et al.*, 2007 ; Grove 2002 ; Hammond *et al.*, 2004 ; Martikainen *et al.*, 2000 ; Simila *et al.*, 2002a ; Simila *et al.*, 2002b ; Stenbacka *et al.*, 2010
Fragmentation forestière / habitats	Brunet et Isaacson 2009 ; Hammond *et al.*, 2004 ; Jonsell *et al.*, 1999 ; Jonsell *et al.*, 2003 ; Jonsson *et al.*, 2003 ; Ranius et Hedin 2001 ; Rukke et Mitgaard 1998

Tableau 7: Revue bibliographique rapide de l'utilisation des coléoptères saproxyliques comme groupe d'étude en forêt.

Les coléoptères saproxyliques seront échantillonnés à l'aide de pièges à interception multidirectionnels de type POLYTRAP. Les objectifs de l'étude ne sont pas compatibles avec l'utilisation de mélanges attractifs pour les pièges. Contrairement à un inventaire, nous ne cherchons pas à contacter un nombre important d'espèces mais uniquement les espèces en relation proche avec le milieu.

Le positionnement du piège a également son importance. Les pièges installés contre (ou proches) des troncs des arbres de fort diamètre et/ou mourants contactent une faune différente de celle de pièges installés entre les arbres dans le même milieu (Svedrup-Thygesson et Birkemoe 2009). Plus d'un piège dans chaque zone devra être installé pour limiter cet effet.

3.2.3. Option GDP (structure spatiale des populations de certaines espèces)

Les études sur la génétique des populations d'insectes en milieu forestier sont nombreuses. Elles sont axées sur les papillons (Habel *et al*., 2010 ; Joyce et Pullin 2003), mais également sur les éphémères (Hogg *et al*., 2002 ; Rebora *et al*., 2005), les libellules (Keller *et al*., 2010) et les coléoptères (Knutsen *et al*., 2000 ; Roslin 2001 ; Whitlock 1996). L'objectif de ces études est variable, et nécessite de ce fait des marqueurs génétiques particuliers en fonction que l'on veuille voir des évolutions rapides ou lentes au niveau des populations ou des individus (Sunnuks 2000). Gomez-Zurita et Galian (2005) ont relevé dans les bases de données génétiques publiques les espèces de coléoptères (Chrysomeloidea et Curculionoidea) sur lesquelles des séquences de gènes ont été décodées. Parmi elles, trois espèces se retrouvent en France et sont saproxyliques. Il s'agit de *Clytus arietis* (Cerambycidae), *Platystomos albinus* (Anthribidae) et *Ips typographus* (Scolytidae).

Plusieurs études ont mis en évidence des flux d'individus conditionnant la structure des populations ou métapopulations d'insectes étudiés (Knutsen *et al*., 2000 ; Roslin 2001 ; Whitlock 1996 ; Keller *et al*., 2010). Dans un cas particulier, la fragmentation de l'habitat met en péril la survie locale d'une espèce de coléoptères saproxylique (Knutsen *et al*., 2000) alors que dans un autre, les capacités de dispersion de l'insecte lui permettent de se maintenir dans un habitat fragmenté (Roslin 2001). En Australie, Watson (2003) a mis en évidence un comportement de dispersion différent en fonction des sexes. Les mâles de *Prostomis atkinsoni* dispersent sur de grandes distances alors que les femelles sont plus sédentaires. Ceci pose le problème de la colonisation de nouveaux patches d'habitat dans un environnement fortement fragmenté (Gyllestrand et Seppa 2003).

Les possibilités d'étude apportées par l'outil qu'est la génétique sont immenses. Des phénomènes populationnels difficiles -sinon impossibles- à observer par des moyens « traditionnels » peuvent être clairement mis en évidence (Watson 2003).

Cependant, l'approche génétique n'est pas sans contraintes. Dans notre cas d'étude précis, elle se heurte à deux obstacles principaux :

- (1) Le choix d'une ou des espèce(s) saproxylique(s). La ou les espèces doivent être sensibles à la fragmentation de leur habitat. Pourtant, choisir des espèces très sensibles à la fragmentation n'est pas judicieux. On ne les retrouverait pas dans les zones fortement fragmentées, et il serait alors impossible de discuter de la structuration spatiale des populations de ces espèces. De plus, elles doivent être échantillonnables en nombre suffisant pour permettre des analyses génétiques. Watson (2003) a collecté manuellement plus d'une centaine d'individus adultes et un peu moins de 400 larves de *P.atkinsoni* pour des analyses génétiques sur 16 sites d'étude, soit un total de plus de 500 individus !

- (2) Le développement de marqueurs génétiques spécifiques à une espèce, la réalisation des manipulations, l'utilisation des appareillages adéquats et l'analyse des données obtenues sont autant de facteurs nécessitant des collaborations avec des partenaires ou sous-traitants extérieurs au projet pour l'instant.

4. Lien avec d'autres projets

Ce projet n'est pas une initiative isolée pour étudier les relations entre vieillissement et biodiversité saproxylique. D'autres projets connexes auxquels participe le Cemagref de Nogent-sur-Vernisson sont présentés succinctement :

En lien avec Q1 : Distrafor**:** L'objectif général de ce projet porte sur l'influence de la trame forestière actuelle et ancienne sur la dynamique spatiale de la biodiversité forestière à travers trois volets complémentaires.

En lien avec Q2 : Thèse d'Aurore Lassauce **:** Le programme de thèse vise à mieux connaître les conséquences pour l'entomofaune saproxylique de l'intensification de la récolte des houppiers, des arbres-entiers, des rémanents forestiers et du vieillissement des TSF et de la futaie.

En lien avec Q2 : Projet GNB : Le projet a pour but d'étudier le lien entre biodiversité, exploitation forestière et naturalité, en comparant des parcelles exploitées à des parcelles non exploitées (Réserves Biologiques, Réserves Naturelles).

En lien avec Q3 : Forgeco : Dans ce projet, des développements méthodologiques importants sont attendus dans les domaines de la modélisation forestière (changement d'échelle, généricité), de la relation entre historique de gestion et biodiversité, de l'étude de viabilité, de l'analyse par la méthode des frontières de production et de la gestion participative.

5. Application des résultats

La compréhension du rôle et du fonctionnement des peuplements sur matures vis-à-vis des coléoptères saproxyliques va permettre d'améliorer les préconisations de mise en place et de gestion des îlots de vieux bois en forêt. La taille et la distance minimale entre les IVB sera également mieux définie pour leur permettre de jouer pleinement leur rôle de « bateau de sauvetage » (Matveinen-Huju *et al*., 2006) pour la biodiversité saproxylique.

Le rôle des différents éléments non forestiers constitutifs de la TTVB sera également mieux appréhendé et permettra d'émettre des recommandations pour optimiser leur répartition spatiale au niveau national pour améliorer la connectivité de la TTVB.

8. Bibliographie

Addison, J. (2007). "Green Tree Retention: A Tool to Maintain Ecosystem Health and Function in Second-Growth Coastal Forests." Arthropods of Canadian Forests 3: 6-9.

Andersson, L. et R. Kriukelis (2002). Pilot Woodland Key Habitat Inventory in Lithuania. Vilnius, Forest Department, Ministry of Environment, Lithuania Regional Forestry Board of Östra Götaland, Sweden: 132.

Aubry, K. B., C. B. Halpern, et al. (2004). "Ecological effects of variable-retention harvests in the northwestern United States: the DEMO study." Forest Snow and Landscape Research 78(1/2): 119-137.

Aubry, K. B., C. B. Halpern, et al. (2009). "Variable-retention harvests in the Pacific Northwest: A review of short-term findings from the DEMO study." Forest Ecology and Management 258: 398-408.

Aubry, K. B., M. P. Amaranthus, et al. (1999). "Evaluating the Effects of Varying Levels and Patterns of Green-tree Retention: Experimental Design of the DEMO Study." Northwest Science 73(Special Issue).

Aune, K., B. G. Jonsson, et al. (2005). "Isolation and edge effects among woodland key habitats in Sweden: Is forest policy promoting fragmentation?" Biological Conservation 124: 89-95.

Baldi, A. et J. Vörös (2006). "Extinction debt of Hungarian reserves: A historical perspective." Basic and Applied Ecology 7: 289-295.

Berg, A., U. Gärdenfors, et al. (2002). "Habitat preferences of red-listed fungi and bryophytes in woodland key habitats in southern Sweden – analyses of data from a national survey." Biodiversity and conservation 11: 1479-1503.

Borges, A., B. Mériguet, et al. (2005). PARCS DÉPARTEMENTAUX DE SEINE-SAINT-DENIS : Parc de la Courneuve, Parc du Sausset, Parc de la Haute Île, Parc de l'Île-Saint-Denis, Parc Jean Moulin – Les Guillands. OPIE. Guyancourt: 63.

Borges, A., B. Meriguet, et al. (2006). Inventaire Entomologique – Parcs départementaux de Seine Saint-Denis. OPIE. Guyancourt.

Boudreault, C., Y. Bergeron, et al. (2002). "Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada." Canadian Journal of Forest Research 32: 1080-1093.

Bouget, C. (2008). Diversité des insectes des forêts humides: Enjeux de conservation et de gestion. Les insectes en zones humides continentales, Monthieux (Dombes, Ain), Fondation Pierre Vérots.

Bouget, C. et H. Brustel (2010). Continuité des micro-habitats dans l'espace et le dans le temps et conservation de l'entomofaune saproxylique. Biodiversité, naturalité, humanité - Pour inspirer la gestion des forêts. D. Vallauri, J. André, J. C. Genet, J. P. de Palma et R. Eynard-Machet. Paris, Tech&Doc, Lavoisier: 51-58

Bouget, C. et L.-M. Nageleisen (2009). L'étude des insectes en forêt: méthodes et techniques, éléments essentiels pour une standardisation. Paris, ONF Les dossiers forestiers.

Boureau, J. G., C. Foyer-Bénos, et al. (2005). "Le paysage forestier vu du ciel." L'If, IFN 10: 12.

Brunet, J. et G. Isacsson (2009). "Restoration of beech forest for saproxylic beetles—effects of habitat fragmentation and substrate density on species diversity and distribution." Biodiversity and Conservation 18: 2387-2404.

Brustel, H. (2004). Coléoptères saproxyliques et valeur biologique des forêts française. Institut National Polytechnique. Toulouse. Doctoral thesis: 297.

Carpaneto, G. M., A. Mazziotta, et al. (2010). "Conflict between insect conservation and public safety: the case study of a saproxylic beetle (Osmoderma eremita) in urban parks." Journal of Insect conservation 14: 555-565.

Cinotti, B. (1996). "Évolution des surfaces boisées en France : Proposition de reconstitution depuis le début du XIXe siècle." Revue forestière Française XLVIII(6): 547-562.

Comité des Ministres (1988a). "RECOMMANDATION N° R (88) 10 DU COMITÉ DES MINISTRES AUX ÉTATS MEMBRES POUR LA CONSERVATION DES ORGANISMES SAPROXYLIQUES ET LEURS BIOTOPES (adoptée par le Comité des Ministres le 13 juin 1988, lors de la 418e réunion des Délégués des Ministres)."

Comité des Ministres (1988b). "RECOMMANDATION N° R (88) 11 DU COMITÉ DES MINISTRES AUX ÉTATS MEMBRES RELATIVE AUX FORÊTS ANCIENNES NATURELLES ET SEMI-NATURELLES (adoptée par le Comité des Ministres le 13 juin 1988, lors de la 418e réunion des Délégués des Ministres)."

Conseil de l'Europe (2003). Déclaration sur le réseau écologique paneuropéen. 5ème Conférence Ministérielle. Kiev, Ukraine.

Degron, R. et C. Gallemant (1999). "Une intégration maîtrisée des fonctions environnementales dans l'aménagement de la forêt domaniale du Romersberg." Revue forestière Française LI(Numéro spécial): 138-148.

Demesure, B. et J. Musch (2001). "L'évolution de la forêt française après la dernière glaciation : l'apport de la palynologie, l'archéologie et de la biologie moléculaire." Dossier de l'environnement de l'INRA 21: 23-28.

Déry, S. et M. Leblanc (2005). Lignes directrices pour l'implantation des îlots de vieillissement rattachées à l'objectif sur le maintien de forêts mûres et surannées - Partie II : intégration à la planification forestière. Gouvernement du Québec. Québec, ministère des Ressources naturelles et de la Faune Direction de l'environnement forestier: 18.

Dubois, G. (2009). Écologie des coléoptères saproxyliques : Biologie des populations et conservation d'Osmoderma eremita (Coleoptera : Cetoniidae). U.M.R. 6553 ECOBIO. Rennes, Université de Rennes1: 216.

Dunn, R. R. (2000). "Isolated trees as foci of diversity in active and fallow fields." Biological Conservation 95: 317-321.

Dupouey, J.-L., J. Bachacou, et al. (2007). "Vers la réalisation d'une carte géoréférencée des forêts anciennes de france." Le Monde des Cartes 191: 85-98.

Ehrlich, P. R. (1988). The loss of diversity: causes and consequences. Biodiversity. E. O. Wilson. Washington D.C., National Academic press: 21-27.

Ek, T. et R. Bermanis (2004). Woodland key habitat concentration - Survey method. Riga, State Forest Service, Latvia: 32.

Ericsson, T. S., H. Berglund, et al. (2005). "History and forest biodiversity of woodland key habitats in south boreal Sweden." Biological conservation 122: 289-303.

Fan, J., J. Sun, et al. (2007). "Attraction of the Japanese pine sawyer, Monochamus alternatus, to volatiles from stressed host in China." Annals of Forest Science 64: 67-71.

Fan, Z., S. R. Shifley, et al. (2003). "Distribution of cavity trees in midwestern old-growth and second-growth forests." Canadian Journal of Forest Research 33: 1481-1494.

Gagnon, E. et G. Gangbazo (2007). Efficacité des bandes riveraines : analyse de la documentation scientifique et perspectives. Ministère du Développement durable de l'Environnement et des Parcs. Direction des politiques de l'eau. Québec. 7: 17.

Galindo-Cardona, A., T. Giray, et al. (2007). "Bess Beetle (Coleoptera: Passalidae): Substrate Availability, Dispersal, and Distribution in a Subtropical Wet Forest." Ecology and Population Biology 100(5): 711-720.

Gibb, H., J. Hjältén, et al. (2006a). "Wing loading and habitat selection in forest beetles: Are red-listed species poorer dispersers or more habitat-specific than common congenerics?" Biological Conservation 132: 250-260.

Gibb, H., J. Hjältén, et al. (2006b). "Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages." Ecography 29: 191-204.

Giblin-Davis, R. M., T. J. Weissling, et al. (1994). "Field response of Rhynchophorus cruentatus (Coleoptera: Curculionidae) to its aggregation pheromone and fermenting plant volatiles." Florida Entomologist 77(1): 164-177.

Gilg, O. (2005). "Old-growth forests: Characteristics, conservation and monitoring (Atelier technique des espaces naturels)." Habitat and species management Technical report n°74 bis: 96 p.

Gjerde, I., M. Saetersdal, et al. (2004). "Fine-Scale Diversity and Rarity Hotspots in Northern Forests." Conservation Biology 18(4): 1032-1042.

Gomez-Zurita, J. et J. Galian (2005). "Current knowledge on genes and genomes of phytophagous beetles (Coleoptera: Chrysomeloidea, Curculionoidea): a review." European Journal of Entomology 102: 577-597.

Götmark, F. (2009). "Conflicts in conservation: Woodland key habitats, authorities and private forest owners in Sweden." Scandinavian Journal of Forest Research 24(6): 504-514.

Gove, A. D., J. D. Majer, et al. (2009). "Ant assemblages in isolated trees are more sensitive to species loss and replacement than their woodland counterparts." Basic and Applied Ecology 10: 187-195.

Grove, S. J. (2002). "The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest." Biological Conservation 104: 149-171.

Gustafsson, L. (2000). "Red-listed species and indicators: vascular plants in woodland key habitats and surrounding production forests in Sweden." Biological Conservation 92: 35-43.

Gustafsson, L., J. de Jong, et al. (1999). "Evaluation of Swedish woodland key habitats using red-listed bryophytes and lichens." Biodiversity and conservation 8: 1101-1114.

Gustafsson, L., J. Kouki, et al. (2010). "Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences." Scandinavian Journal of Forest Research 25: 295-308.

Gyllenstrand, N. et P. Seppa (2003). "Conservation genetics of the wood ant, Formica lugubris in a fragmented landscape." Molecular Ecology 12(11): 2931-2940.

Habel, J. C., A. Finger, et al. (2010). "Survival of the endangered butterfly Lycaena helle in a fragmented environment: Genetic analyses over 15 years." Journal of Zoological Systematics and Evolutionary Research 49(1): 25-31.

Haddad, N. M. (2000). "Corridor lenght and Patch Colonisation by a Butterfly, Junonia coenia." Conservation Biology 14(3): 738-745.

Hammond, H. E. J., D. W. Langor, et al. (2004). "Saproxylic beetles (Coleoptera) using Populus in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages." Canadian Journal of Forest Research 34: 1-19.

Hanski, I. et O. Ovaskainen (2002). "Extinction Debt at Extinction Threshold." Conservation Biology 16(3): 666-673.

Hautala, H., J. Jalonen, et al. (2004). "Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland." Biodiversity and conservation 13: 1541-1554.

Hautala, H., S. Laaka-Lindberg, et al. (2009). "Effects of Retention Felling on Epixylic Species in Boreal Spruce Forests in Southern Finland." Restoration Ecology: 1-12.

Hazell, P. et L. Gustafsson (1999). "Retention of trees at final harvest - evaluation of a conservation technique using epiphytic bryophyte and lichen transplants." Biological Conservation 90: 133-142.

Hedenas, H. et P. Hedström (2007). "Conservation of epiphytic lichens: Significance of remnant aspen (Populus tremula) trees in clear-cuts." Biological Conservation 135: 388-395.

Hedin, J., T. Ranius, et al. (2008). "Restricted dispersal in a flying beetle assessed by telemetry." Biodiversity and conservation 17: 675-684.

Hilszczański, J., H. Gibb, et al. (2005). "Parasitoids (Hymenoptera, Ichneumonoidea) of Saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest." Biological Conservation. 126: 456-464.

Hogg, I. D., P. Willmann-Huerner, et al. (2002). "Population genetic structures of two New Zealand stream insects: Archichauliodes diversus (Megaloptera) and Coloburiscus humeralis (Ephemeroptera)." New Zeland Journal of Marine and Freshwater Research 36: 491-501.

Hottola, J. et J. Siitonen (2008). "Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests." Biodiversity and Conservation 17: 2559-2577.

Hunter, M. D. (2002). "Landscape structure, habitat fragmentation, and the ecology of insects." Agricultural and Forest Entomology 4: 159-166.

Hyvarinen, E., J. Kouki, et al. (2009). "Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups." Insect Conservation and Diversity 2: 93-105.

IFN (2011). http://www.ifn.fr/. Consulté le 25 Février 2011

Jairus, K., A. Löhmus, et al. (2009). "Lichen acclimatization on retention trees: a conservation physiology lesson." Journal of Applied Ecology 46: 930-936.

Johansson, P. et L. Gustafsson (2001). "Red-listed and indicator lichens in woodland key habitats and production forests in Sweden." Canadian Journal of Forest Research 31: 1617-1628.

Jonsell, M. (2004). "Old park trees: A higly desirable ressource for both history and beetle diversity." International Society of Arboriculture 30(4): 238-244.

Jonsell, M., G. Nordlander, et al. (1999). "Colonization patterns of insects breeding in wood-decaying fungi." Journal of Insect Conservation 3: 145-161.

Jonsell, M., M. Schroeder, et al. (2003). "The saproxylic beetle Bolitophagus reticulatus: its frequency in managed forests, attraction to volatiles and flight period." Ecography 26

Jonsson, M., J. Johannesen, et al. (2003). "Comparative Genetic Structure of the Threatened Tenebrionid Beetle Oplocephala haemorrhoidalis and its Common Relative Bolitophagus reticulatus " Journal of Insect Conservation 7(2).

Joyce, D. A. et A. S. Pullin (2003). "Conservation implications of the distribution of genetic diversity at different scales: a case study using the marsh fritillary butterfly (Euphydryas aurinia)." Biological Conservation 114: 453-461.

Keller, D., S. Brodbeck, et al. (2010). "Ecological and genetic measurements of dispersal in a threatened dragonfly." Biological Conservation 143(2658-2663).

Kirby, K. J., R. C. Thomas, et al. (1995). "Pasture-woodland and its conservation in Britain." Biological Journal of the Linnean Society 56: 135-153.

Knutsen, H., B. A. Rukke, et al. (2000). "Genetic differentiation among populations of the beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae) in a fragmented and a continuous landscape." Heredity 84: 667-676.

Laaksonen, M., E. Peuhu, et al. (2008). "Effects of habitat quality and landscape structure on saproxylic species dwelling in boreal spruce-swamp forests." Oikos 117: 1098-1110.

Lachat, T. et R. Bütler (2007). Gestion des vieux arbres et du bois mort. Îlots de sénescence, arbres-habitat et métapopulations saproxyliques. Mandat de l'Office fédéral de l'environnement. Lausanne: 87.

Laita, A., M. Mönkkönen, et al. (2010). "Woodland key habitats evaluated as part of a functional reserve network." Biological Conservation 143: 1212-1227.

Lanier, L. (1986). Précis de sylviculture. Nancy, ENGREF.468p

Leseigneur, L. (1972). Coléoptères Elateridae de la faune de France continentale et de Corse. Bulletin mensuel de la Société linnéenne de Lyon, suppl. février 1972.

Löhmus, A. et P. Löhmus (2010). "Epiphyte communities on the trunks of retention trees stabilise in 5 years after timber harvesting, but remain threatened due to tree loss." Biological Conservation 143: 891-898.

Lumsden, L. F. and A. F. Bennett (2005). "Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia." Biological Conservation 122: 205-222.

Maguire, D. A., C. B. Halpern, et al. (2007). "Changes in forest structure following variable-retention harvests in Douglas-fir dominated forests." Forest Ecology and Management 242: 708-726.

Martikainen, P., J. Kouki, et al. (2006). "The effects of green tree retention and subsequent prescribed burning on ground beetles (Coleoptera: Carabidae) in boreal pine-dominated forests." Ecography 29: 659-670.

Martikainen, P., J. Siitonen, et al. (2000). "Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland." Biological Conservation 94: 199-209.

Matveinen-Huju, K., J. Niemelä, et al. (2006). "Retention-tree groups in clear-cuts: Do they constitute 'life-boats' for spiders and carabids?" Forest Ecology and Management 230: 119-135.

Mazurek, M. J. et W. J. Zielinski (2004). "Individual legacy trees influence vertebrate wildlife diversity in commercial forests." Forest Ecology and Management 193(3): 321-334.

McGeoch, M. A., M. Schröder, et al. (2007). "Saproxylic beetles diversity in a managed boreal forest: importance of stand characteristics and forestry conservation measures " Diversity and Distributions 13(4): 418-429.

Mériguet, B. et P. Zagatti (2004). Inventaire entomologique au Bois de Saint Eutrope. OPIE. Guyancourt: 34.

Michel, A. K. et S. Winter (2009). "Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A." Forest Ecology and Management 257: 1453-1464.

Moning, C. et J. Müller (2009). "Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (Fagus sylvatica L.) dominated forests." Ecological Indicators 9: 922-932.

Moorman, C. E., K. R. Russell, et al. (1999). "Snag dynamics and cavity occurrence in the South Carolina Piedmont." Forest Ecology and Management 118: 37-48.

Mourey, J.-M. et J. Touroult (2010). Les arbres à conserver pour la biodiversité Comment les identifier et les désigner ? Fiche Technique-Biodiversité. ONF, Paris. 3: 7.

Nascimbene, J., L. Marini, et al. (2010). "Epiphytic lichen diversity in old-growth and managed Picea abies stands in Alpine spruce forests." Forest Ecology and Management 260: 603-609.

Nilsson, S. G., M. Niklasson, et al. (2003). "Erratum to ''Densities of large living and dead trees in old-growth temperate and boreal forests''." Forest Ecology and Management 178: 355-370.

Norse, E. A., K. L. Rosenbaum, et al. (1986). Conserving biological diversity in our national forests. Washington D.C.

Ohsawa, M. (2007). "The role of isolated old oak trees in maintaining beetle diversity within larch plantations in the central mountainous region of Japan." Forest Ecology and Management 250: 215-226.

ONF (2005). Ilots de vieillissement: mode d'emploi - Pourquoi et comment installer des îlots de vieillissement dans les forêts du Morvan? Bougogne & Champagne-Ardennes: 25.

ONF (2009a). Conservation de la biodiversité dans la gestion courante des forêts publiques. INS-09-T-71: 11.

ONF (2009b). Îlots de vieux bois. NDS-09-T-310: 6.

ONF (2009c). Modalité de désignation des coupes et contrôle de l'exploitation. INS-09-T-69: 7.

Penttilä, R., J. Siitonen, et al. (2004). "Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland." Biological Conservation 117: 271-283.

Perhans, K., L. Appelgren, et al. (2009). "Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes." Biological Conservation 142: 1125-1133.

Piégay, H., G. Pautou, et al. (2003). Les forêts riveraines des cours d'eau: écologie, fonction, gestion. Paris.

Pitkänen, A., K. Törmänen, et al. (2005). "Effects of green tree retention, prescribed burning and soil treatment on pine weevil (Hylobius abietis and Hylobius pinastri) damage to planted Scots pine seedlings." Agricultural and Forest Entomology. 7: 1-12.

Pointereau, P. (2001). Evolution du linéaire de haies en France durant ces 40 dernières années : l'apport et les limites des données statistiques. Hedgerows of the world, their ecological functions in different lanscapes. Birmingham.

Pointereau, P. et F. Coulon (2006). La haie en France et en Europe : évolution ou régression, au travers des politiques agricoles. PREMIÈRES RENCONTRES NATIONALES DE LA HAIE CHAMPÊTRE. Auch.

Ranius, T. et J. Hedin (2001). "The dispersal rate of a beetle, Osmoderma eremita, living in tree hollows." Oecologia 126: 363-370.

Rebora, M., L. Lucentini, et al. (2005). "Genetic differentiation among populations of Baetis rhodani (Ephemeroptera, Baetidae) in three Italian streams." Italian Journal of Zoology 72(2): 121-126.

Robert, P. (1977). Dictionnaire alphabétique et analogique de la langue Française. Paris.2171p

Rose, C. R. et P. S. Muir (1997). "Green-tree retention: Consequences for Timber Pruduction in Forests of the Western Cascades, Oregon." Ecological Applications 7(1): 209-217.

Rosenvald, R. et A. Lömhmus (2008). "For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects." Forest Ecology and Management 255: 1-15.

Roslin, T. (2001). "Spatial population structure in a patchily distributed beetle." Molecular Ecology 10: 823-837.

Rouveyrol, P. (2009). Caractérisation d'un îlot idéal de vieux arbres en forêt de montagne. ENGREF. AgroParisTech. Paris: 185.

Rukke, B. A. et F. Midtgaard (1998). "The importance of scale and spatial variables for the fungivorous beetle Bolitophagus reticulatus (Coleoptera, Tenebrionidae) in a fragmented forest landscape." Ecography 21: 561-572.

Sahlin, E. et L. M. Schroeder (2010). "Importance of habitat patch size for occupancy and density of aspen-associated saproxylic beetles." Biodiversity and conservation 19: 1325-1339.

Schroeder, L. M., T. Ranius, et al. (2007). "Spatial occurrence of a habitat-tracking saproxylic beetles inhabiting a managed forest landscape." Ecological Applications 17(3): 900-909.

Siitonen, J. and L. Saaristo (2000). "Habitat requirements and conservation of Pytho kolwensis, a beetle species of old-growth boreal forest." Biological Conservation 94: 211-220.

Siitonen, J., J. Hottola, et al. (2009). "Differences in Stand Characteristics Between Brook-Side Key Habitats and Managed Forests in Southern Finland." Silva Fennica 43(1): 21-37.

Siitonen, J., P. Martikainen, et al. (2000). "Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland." Forest Ecology and Management 128: 211-225.

Similä, M., J. Kouki, et al. (2002a). "Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages." Biological Conservation 106: 19-27.

Similä, M., J. Kouki, et al. (2002b). "Beetle species richness along the forest productivity gradient in northern Finland." Ecography 25: 42-52.

Sippola, A.-L., M. Mönkkönen, et al. (2005). "Polypore diversity in the herb-rich woodland key habitats of Koli National Park in eastern Finland." Biological Conservation 126: 260-269.

Speight, M. C. D. (1989). Les invertébrés saproxyliques et leur protection. Collection sauvegarde de la nature. Strasbourg, Conseil de l'Europe. 42: 77.

Stenbacka, F., J. Hjältén, et al. (2010). "Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity." Ecological Applications 20(8): 2310-2321.

Sunnuks, P. (2000). "Efficient genetic markers for population biology." TREE 15(5): 199-203.

Sverdrup-Thygeson, A. et F. Midtgaard (1998). "Fungus-infected trees as islands in boreal forest: Spatial distribution of the fungivorous beetle Bolitophagus reticulatus (Coleoptera, Tenebrionidae)." Ecoscience 5(4): 486-493.

Sverdrup-Thygeson, A. et R. A. Ims (2002). "The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen." Biological Conservation 106: 347-357.

Sverdrup-Thygeson, A. et T. Birkemore (2009). "What window traps can tell us: effect of placement, forest openness and beetle reproduction in retention trees." Journal of Insect conservation 13: 183-191.

Telleria, J. L., R. Baquero, et al. (2003). "Effects of forest fragmentation on European birds: implications of regional differences in species richness." Journal of Biogeography 30: 621-628.

Témoin, J.-L. (2009). Mise en place d'un réseau d'îlots de vieux bois en forêt domaniale de Rambouillet. Rambouillet: 24.

Tilman, D., R. M. May, et al. (1994). "Habitat destruction and the extinction debt." Nature 371: 65-66.

Timonen, J., J. Siitonen, et al. (2010). "Woodland key habitats in northern Europe: concepts, inventory and protection." Scandinavian Journal of Forest Research 25: 309-324.

Tittler, R., S. J. Hannon, et al. (2001). "Residual tree retention ameliorates short-term effects of clear-cutting on some boreal songbirds." Ecological applications 11(6): 1656-1666.

Tositti, A. (2004). Îlots de vieux bois. Tec. Rept. Institut d'Aménagement et d'Urbanisme de la région Ile-de-France.

Tositti, A. et B. Cauchetier (2005). "Le vieux bois, élément essentiel de la biodiversité forestière." Note rapide sur l'Environnement, IAURIF 396: 6.

Triantis, K. A., P. A. V. Borges, et al. (2010). "Extinction debt on oceanic islands." Ecography 33: 285-294.

Vanha-Majamaa, I. et J. Jalonen (2001). "Green Tree Retention in Fennoscandian Forestry." Scandinavian Journal of Forest Research 16(2): 79-90.

Vignon, V. (2006). Les trognes: Un habitat de substitution remarquable pour les coléoptères saproxyliques. 1er Colloque Européen sur les trognes. Vendôme.

Wagner, S., I. Herrmann, et al. (2010). "Spatial optimization for dispersion of remnant trees in seed-tree cuttings and retention-tree stands of Scots pine." Scandinavian Journal of Forest Research 25(5): 432-445.

Watson, S. (2003). Dispersal and gene flow in Prostomis atkinsoni (Coleoptera). Melbourne, La Trobe University: 58.

Werner, F. A. (2010). "Reduced growth and survival of vascular epiphytes on isolated remnant trees in a recent tropical montane forest clear-cut." Basic and Applied Ecology: Article in press doi:10.1016/j.baae.2010.11.002.

Whitlock, M. C. (1992). "Nonequilibrium population structure in forked fungus beetles: Extinction, colonization, and thd genetic variance among populations." The American Naturalist 139(5): 952-970.

Wilcox, B. A. et D. D. Murphy (1985). "Conservation strategy: the effects of fragmentation on extinction." American Naturalist 125: 879-887.

Williams, W. I. et I. C. Robertson (2008). "Using automatedflight mills to manipulate fat reserves in Douglas-fir beetles, Dendroctonus pseudotsugae (Hopkins)(Coleoptera: Curculionidae)." Environmental Entomology 37: 850-856.

Wolff, J. O., E. M. Schauber, et al. (1997). "Effects of habitat loss and fragmentation on the behavior and demography of Gray-Tailed Voles." Conservation Biology 11(4): 945-956.

Work, T. T., J. M. Jacobs, et al. (2010). "High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests." Ecological Applications 20(3): 741-751.

Zenner, E. K. (2000). "Do Residual Trees Increase Structural Complexity in Pacific Northwest Coniferous Forests?" Ecological Applications 10(3): 800-810.

Zenner, E. K. (2004). "Does old-growth condition imply high live-tree structural complexity?" Forest Ecology and Management 195: 243-258.

Annexe 4 : Versions pdf des articles publiés

Article 1: Influence of sampling effort on saproxylic beetle diversity assessment: implications for insect monitoring studies in European temperate forests

Agricultural and Forest Entomology

Agricultural and Forest Entomology (2013), **15**, 135–145 DOI: 10.1111/afe.12008

Influence of sampling effort on saproxylic beetle diversity assessment: implications for insect monitoring studies in European temperate forests

Guilhem Parmain*†‡, Marc Dufrêne§¶, Antoine Brin and Christophe Bouget‡**

**National Laboratory of Forest Entomology, National Forest Office (ONF), 2 rue Charles Péguy, F-11500 Quillan, France, †Natural Patrimony Department, National Museum of Natural History, 36 rue Geoffroy St Hilaire, CP 41 75 231 Paris Cedex 05, France, ‡'Forest Ecosystems' Research Unit, National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), Domaine des Barres, F-45290 Nogent-sur-Vernisson, France, §Department of Natural and Rural Environnement Monitoring (SPW/DGARNE/DEMNA), Avenue Maréchal Juin 23, B-5030 Gembloux, Belgium, ¶Liege University, Gembloux Agro Bio Tech (GxABT) Forests, Nature, Landscape Department Passage des Déportés, 2, B 5030 Gembloux, Belgium, and **Purpan Engineering School, University of Toulouse, UMR INPT/INRA 1201 Dynafor, 75 voie du T.O.E.C., BP 57611, F-31076, Toulouse Cedex 03, France*

Abstract

1 Saproxylic beetle diversity monitoring provides a tool for estimating the efficiency of forest conservation measures. Flight interception traps are commonly employed to monitor beetle assemblages, although little explicit knowledge of the efficiency of this trapping method is available.

2 The present study investigated how slight changes in sampling effort can influence species richness and species composition of assemblages in data sets from standard window-flight traps.

3 At both trap and plot levels, an additional year or an additional trap provided a 50% increase in the number of species detected (a 75% increase for rare species) and resulted in a different estimated composition of the assemblages. Adding 2 or 3 years of sampling gave twice as many species and resulted in assemblages that were 50% dissimilar. Increases in the detection of species and the dissimilarity of assemblages were similarly affected along a gradient of forest conditions, suggesting that changes in sampling effort were not affected by forest condition.

4 At the forest level, year or trap replication provided smaller increases in species richness (31% and 25%, respectively). Within sites, distance measures in species composition between traps did not differ significantly when based on 1 or 2 years of data. Using two traps per plot compared with one trap influenced comparisons between stand types, based on species richness, in 25% of the cases.

5 Species detection was similarly increased by either year replication or trap replication. The results of the present study highlight the significant role played by finescale patterns of habitat structure and inter-annual variation with respect to determining catch size and assemblages of saproxylic species.

Keywords Biodiversity, dissimilarity, flight-interception trap, replication, species richness.

Introduction

Saproxylic organisms, comprising a functional group that depends on dead or dying wood (Alexander, 2008), have been used in Europe (as indicators of forest biodiversity (Nieto & Alexander, 2010) ever since the preservation of forest biodiversity associated with dead wood was recommended by the European Council in 1988 (Comité des Ministres, 1988a, b). They are also used as a tool for estimating the efficiency of forest conservation measures in several countries around the world (Grove, 2002b; Hammond *et al*., 2004; Lachat *et al*., 2006; Ohsawa, 2007). Approximately 30% of European species that depend on forest habitats need dead wood to some extent (Stokland *et al*., 2004). Globally, the

Correspondence: Christophe Bouget; Tel.: (00-33) 23 895 0542; fax: (00-33) 23 895 0359; e-mail: christophe.bouget@irstea.fr

saproxylic biota is species rich (Grove, 2002a), although many species are threatened by loss and fragmentation of habitats with sufficient dead wood and veteran trees.

Beetles account for a large proportion of saproxylic biodiversity [e.g. approximately 25% of the saproxylic species in Scandinavia (Stokland *et al*., 2004), second to fungi]. Foresters and conservationists are paying more attention to them than to saproxylic fungi or Diptera for both practical and ecological reasons. Many beetle species have high conservation value; 11% of species are considered as threatened at the European level (Nieto & Alexander, 2010) and they are assumed to provide valuable information on the quality and continuity of woodland habitats (Grove, 2002b).

If saproxylic beetle diversity is to be used effectively as a management tool in forestry, more explicit knowledge about the efficiency of trapping strategies is needed. A sound beetle sampling strategy should focus on: (i) the choice of an efficient and standardized method, (ii) the timing of samples; and (iii) the spatial framework. Regarding the first point, window (flight interception) traps are widely employed for catching active flying saproxylic beetles (Økland, 1996; Wikars *et al*., 2005; Alinvi *et al*., 2006) because they are easy to replicate and standardize, and are assumed to represent local saproxylic beetle communities that could only be obtained with much more effort using active or extraction methods such as bark peeling, dead wood beating and emergence trapping (Siitonen, 1994; Økland, 1996; McIntosh *et al*., 2001; Alinvi *et al*., 2006; Hyvärinen *et al*., 2006).

In most studies of saproxylic beetles, species richness (SR) estimates are commonly compared based on data from only on a single trapping year, although little is known about the errors involved. Martikainen and Kouki (2003) emphasized the importance of having large sample sizes (more than 200 species) when studying threatened species. Larger samples can be obtained by increasing the number of traps, by sampling for several years or by combining these two approaches. Using a variety of existing data from entomological surveys based on multiple-trap plots in France and Belgium, we assessed the variation in species richness and species composition (evaluated in terms of Sorensen dissimilarity) of the saproxylic beetle assemblages caught with standard window traps (Brustel, 2004) when traps or years of sampling were added. The available data were limited in range (3 years, two traps per plot at most), although they covered a wide range of forest conditions. The present study aimed to determine:

- How does an increase in local sampling effort (increasing the number of traps or yearly replication per plot) affect the assessment of species richness and assemblage composition at the trap, plot and forest level?
- Does the influence of sampling effort on the quality of biodiversity data vary with forest conditions?
- What are the contributions of trap replication exclusively, year replication exclusively and the combination of trap and year replication to variation in estimates of specie richness?
- Does an increased local sampling effort affect the results of ecological comparisons between stand types at the forest level?

Materials and methods

The window trap dataset

In the present study, we used datasets compiled using saproxylic beetles obtained from several biodiversity surveys and ecological studies carried out from 1999 to 2010 by different French organizations National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), National Forest Office (ONF), University of Toulouse-Purpan Engineering School (EIP), Office for Insects and their Environment (OPIE)] and DEMNA (Departement of Natural and Rural Environnement Monitoring) in Belgium.

We only compiled data originating from unbaited or ethanol-baited (methylated spirit, 20%) window traps, suspended approximately 1.5 m above the ground. The trap was the basic sampling unit; at most, two traps, located approximately 20–60 m apart, were grouped to represent captures from the same plot (i.e. the same forest stand). Plots were grouped in sites, which were forests or a cluster of close forests dedicated to the same research project. When several trapping years were available for a given plot, we included only data from consecutive years.

We divided the overall dataset into three subsets to analyze the effects of replication on saproxylic beetle diversity assessments (species richness and assemblage composition) after aggregating the data at three spatial scales (trap, plot and forest): (i) the Multi-Year-Trap set (MYT) at the trap level, to study the effects of year replication (one trap sampled over several years), (ii) the Multi-Trap-Plot set (MTP) at the plot level, to study the effects of trap replication (two traps; i.e. one additional trap located near the first, and sampled one single year) and (iii) the Multi-Trap-Multi-Year-Plot set (MTMYP), at the trap and plot levels, to compare the relative effects of trap and year replications. We also analyzed the consistency of the effects of trap or year replication over spatial scales, by upscaling from the trap/plot to the forest level on selected well-replicated sites.

In the MYT subset, we selected sites in which plots had been sampled at the same place for two or three consecutive years. The MYT dataset contained 72 plots, for a total of 299 traps in 19 sites (Table 1). Six sites (n traps ≥ 10), with 239 traps in 50 plots were selected for analyses at the forest level (at least 10 traps cumulated over the same forest; Table 2).

In the second data subset (MTP), a basic plot consisted of two replicate traps, separated by about 20 m (Bouget & Brustel, 2009) or 60 m (in the ORLEANS and BELGWAL datasets). The MTP dataset included 14 sites for 294 plots and 588 traps (Table 1). Eight sites (n traps ≥ 10), with 257 plots and 514 traps, were selected for analyses at the forest level (Table 3). In the BELGWAL set, we considered only the first two traps in each plot, although the data provided by one of them during the second sampling year were analyzed as a new replicate. An independent analysis of trap replication from one to eight traps using the Belgian set only would be too idiosyncratic, and weakened by the small sample size (22 plots only). At the multiple-plot forest level, we also studied whether trap replication influenced the significance, magnitude and direction of the faunistic differences between stand types. Environmental variables describing the stand type and required to answer a

Table 1 Summary of the dataset used for analyses

Dataset	Site	Number of sampling years	Number of species	Number of traps	Number of plots
MYT	Ballons-Comtois*	3	135	12	6 (6)
MYT	Bannes*	2	101	4	2 (2)
MYT	BelgWal	2	116	176	22
MYT	Chalmessin*	3	106	4	2 (2)
MYT	Chaumes*	2	47	4	2 (2)
MYT	Courneuve	2	85	10	2
MYT	Fontbleau-Opie*	2	77	2	1 (1)
MYT	Haute-Meurthe*	3	134	4	2 (2)
MYT	Hauts-de-Seine*	2	148	16	5 (2)
MYT	Jujols*	2	78	2	1 (1)
MYT	Kertoff*	3	82	2	1 (1)
MYT	Larchant-Marais*	2	102	4	2 (2)
MYT	Lozere*	2	201	16	10 (6)
MYT	Mantet*	2	38	4	2 (2)
MYT	Rnva*	3	85	2	1 (1)
MYT	Sausset	2	105	25	5
MYT	Tourbiere-Charmes*	2	62	4	2 (2)
MYT	Troncais-Onf*	3	162	6	3 (3)
MYT	Vauhalaise*	2	47	2	1 (1)
MTP	Auberive	1	146	48	24
MTP	Belg-Wal	2	81	44	22
MTP	Brie	1	112	28	14
MTP	Caylus	1	93	4	2
MTP	Chaux-Regix	1	57	6	3
MTP	Coppices	1	210	58	29
MTP	Fontainebleau	1	188	50	25
MTP	Landes	1	210	104	52
MTP	Orleans	1	125	42	21
MTP	Orleans-Regix	1	95	6	3
MTP	Rambouillet	1	265	120	60
MTP	Tronçais-CEM	1	190	62	31
MTP	Ventron	1	52	16	8

*Denotes the sites used to compare the number of additional species collected by a second trap in 1-year plots or by a second year of running one trap in 2-year plots. The number of plots used for multi-year comparisons is given in parenthesis in the 'Plot' column.
MTP, multi-trap plots; MYT, multi-year traps.

transversal ecological question (e.g. dead wood poor versus dead wood rich) were available on eight sites only in the MTP set. We used these eight sites to compare managed versus unmanaged stands (Auberive, Fontainebleau), dead wood-poor versus dead wood-rich stands (Rambouillet, BelgWal Year1, BelgWal Year2, Landes) and overmature versus mature stands (Tronçais-CEM, Coppices).

In the third data subset (MTMYP), we selected two-trap 2-year plots from the MYT dataset. We excluded the third year for some sites because a third trap per plot was not available (exept for BELGWAL). This set (i.e. MTMYP) included 16 sites, 36 plots and 72 traps (Table 1). Samples available for this analysis were well distributed over the ecological forest gradients.

Environmental data

Three environmental factors and one methodological factor were used to describe trap features. The environmental variables qualifying trap location were: forest type (three levels: 'conifer', 'deciduous' and 'mixed'), altitudinal group (two levels: 'highland' and 'lowland', with the reference altitude distinguishing the levels being 1000 m above the sea level) and climatic (or biogeographical) domain [four levels according to the ETCB (European Topic Centre on Biological Diversity) (2006): 'alpine', 'atlantic', 'continental', 'continental-Mediterranean']. Data from alpine or Mediterranean regions were insufficient to provide rigorous tests. The use of bait in the trap (methylated spirit, 20%) was the only methodological factor considered (two levels: 'ethanol-baited' and 'unbaited'; Table 3).

Beetle data

The beetle records from different sets first had to be harmonized, both with respect to nomenclature and saproxylic status. We choosed to follow the French database FRISBEE developed by Bouget *et al*. (2008). Only those records from families for which beetles were identified to the species level were used for the present analysis. These included Alleculidae; Anobiidae;

Table 2 Effect of sampling effort per plot (number traps/years) on species richness and assemblage composition at particular sites

		Comparison between 1 and 2 (years per trap or traps per plot)			
	Sites	Number of plots (traps)	SR-Benefit	Mean Mantel statistics r (1 versus 1 + 2)	Mean Mantel statistics r (2 versus 1 + 2)
MYT	Ballons Comtois	6 (12)	24.10%	0.78***	0.47***
	BelgWal	22 (176)	20.21%	0.59***	0.57***
	Courneuve	2 (10)	40.50%	0.60***	0.28*
	Hauts-de-Seine	5 (16)	35.16%	0.52***	0.60***
	Lozère	10 (16)	29.06%	0.86***	0.89***
	Sausset	5 (25)	40.94%	0.80***	0.78***
	Mean		31.66%	0.69	0.60
MTP	Auberive	24 (48)	30.94%	0.64***	0.55***
	Belg-Wal	22 (44)	33.88%	0.58***	0.62***
	Brie	14 (28)	24.44%	0.79***	0.57**
	Coppices	29 (58)	23.89%	0.71***	0.73***
	Fontainebleau	25 (50)	24.50%	0.71***	0.68***
	Rambouillet	60 (120)	27.27%	0.67***	0.65***
	Landes	52 (104)	15.72%	0.81***	0.84***
	Troncais-CEM	31 (62)	19.87%	0.34***	0.60***
	Mean		25.06%	0.66	0.66

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

The mean species richness benefit index (SR-Benefit) (see text) between traps (multi-trap plot; MTP) or years (multi-year trap; MYT) was used to measure the increase in species number caught by one additional trap or year, respectively. Mantel tests (999 permutations) assessed whether within-site between-trap Sörensen distance matrices based, respectively, on single traps/years were correlated with data that included another trap or year, respectively. The number of traps in parenthesis is the total number of traps per site.

Table 3 Number of traps in multi-year trap (MYT) and multi-trap plot (MTP) datasets for each ecological studied factor

Environmental/methodological factors		Number of traps	
Factor	Category	MYT	MTP
Forest type	Conifer	11	89
	Deciduous	250	459
	Mixed	38	40
Altitude	Highland	44	16
	Lowland	255	572
Climatic domain	Alpine[a]	6	0
	Atlantic	57	360
	Continental	220	228
	Continental/Mediterranean[a]	16	0
Bait	Alcohol-baited	82	32
	No	217	556

[a]This category was not considered as a result of its low number of replicates.

Anthribidae; Biphyllidae; Bostrichidae; Bothrideridae; Buprestidae; Cerambycidae; Cerophytidae; Cerylonidae; Ciidae; Cleridae; Cucujidae; Curculionidae (Scolytinae only); Elateridae; Endomychidae; Erotylidae; Eucnemidae; Histeridae; Laemophloeidae; Leiodidae; Lucanidae; Lycidae; Lymexylidae; Melandryidae; Monotomidae; Mycetophagidae; Nitidulidae; Nosodendridae; Oedemeridae; Phloeostichidae; Prostomidae; Pyrochroidae; Salpingidae; Scarabaeidae; Silvanidae; Sphindidae; Tenebrionidae; Tetratomidae; Trogidae; Trogossitidae; Zopheridae. Several beetle families not studied in a majority of the sets were excluded from our analyses: Aderidae, Alexiidae, Cantharidae, Clambidae, Corylophidae, Cryptophagidae, Dasytidae, Dermestidae, Eucinetidae, Latridiidae, Mordellidae, Ptiliidae, Scirtidae, Scraptiidae, Scydmaenidae, Sphaeritidae, Staphylinidae and Throscidae. A total of 643 saproxylic beetle species [507 common species (79%) and 136 rare species (21%)] were present in the studied datas. They belonged to 42 families (or sub-families).

We characterized each species with conservation value (at the country level) either as 'common' (IP = 1 or 2) or 'rare' species (IP = 3 or 4), in accordance with principles discussed by Brustel (2001) and the database FRISBEE (Bouget *et al*., 2008). In this database, each species has a patrimoniality index (i.e. conservation value; IP), in other words its degree of geographical rarity in France, with four levels: (i) common and widely distributed species; (ii) not abundant but widely distributed species, or only locally abundant species; (iii) not abundant and only locally distributed species; and (iv) very rare species (known in less than five localities or in a single 'county' in France). The 'all species' group contains both the 'common' and the 'rare' species.

Statistical analysis

Because the abundance of beetles was not always available, we only considered beetle occurrence for our analyses.We calculated two major indices based strictly on presence-absence data: (i) the mean benefit of SR (SR-Benefit) and (ii) the mean assemblage dissimilarity between traps or years. We defined the SR-Benefit as the percentage increase in species added by a second trap or year, as follows:

General formula:

$$\text{SR-Benefit} = \frac{(\text{SR}_{(1+2)}\text{-SR}_\text{i})}{\text{SR}_\text{i}} \times 100 \qquad (1)$$

with i = year 1 or 2 (MYT subset), or trap 1 or 2 (MTP subset). Mean percentages were calculated over plots, forests or years, depending on the comparison.

Mean assemblage dissimilarity was used to interpret the significance of the additional captures for understanding the assemblages.The assemblage dissimilarity between plots or years was calculated as the Jaccard–Dice–Sörensen index (Oksanen *et al*., 2011).

To test the influence of environmental characteristics and the use of bait in the traps on the species richness benefit, we fit generalized linear mixed models (GLMER) (Bolker *et al*., 2009), assuming a binomial distribution, with site and plot as random factors and including an observation-specific random intercept to account for possible overdispersion (Elston *et al*., 2001).We tested the significance of effects by comparing factorial models and a null model with a likelihood ratio test (LRT). A Tukey's multiple-comparison test was performed to identify where the differences occurred. We set the significant value of the LRT at 0.01% to limit type II errors.

In the MYT within-site between-trap level analyses, we tested the effects of different combinations of 1, 2 and 3-year sampling designs on SR-Benefit and dissimilarity: a second sampling year after the first one (SR-Benefit A), a third sampling year after two first consecutive sampling years (SR-Benefit B) and two additional sampling years after a single first one (SR-Benefit C).

In the same way, the dissimilarity value was calculated among first-year and second-year or third-year samples. Dissimilarity analyses were always conducted with assemblages composed of all species; a potential more restricted analysis of rare species assemblages was not useful as a result of the small proportion of rare species in our data. The same testing strategy as that used for SR-Benefit was applied for dissimilarity. At the forest level, we only considered the first 2 years of sampling to calculate the difference in species richness between one and two sampling years (see general formula): with SR = Specific Richness and y(i) = year of sampling 1 or 2.

We used Mantel tests (method = Spearman, 999 permutations) to test whether within-site between-trap distance matrices based, respectively, on 1- or 2-year data were correlated.

We compared the effect of additional traps within sites in terms of SR-Benefit and dissimilarity values during single years between one- and two-trap plots [SR = Specific Richness; $t(n)$ = trap number] [possible combinations for each plot: $SRt_1 \sim SRt(1+2)$; $SRt_2 \sim SRt(1+2)$].

The effects of methodological and environmental factors were tested with a GLMER, assuming a Gaussian distribution with a $\log+1$ transformation of the raw data. The model was fit with site as a random factor. The dissimilarity value was computed between one-trap and two-trap plots. The same testing strategy as that used for SR-Benefit was applied for dissimilarity [see the general formula above, with SR = Specific Richness and t(i) = trap number 1 or 2]. We used Mantel statistics on one-trap or two-trap data to test whether the distance measures in species composition between traps (i.e. assemblage dissimilarity) was influenced by the number of traps per plot.

To evaluate the contribution of each replication mode (trap or year) to total species richness, we partitioned the increase in richness observed in the MTMYP dataset into 'exclusive' (species contacted by one mode of replication only) and 'interactive' (species contacted by both modes of replication) effects of trap or year replication by a method adapted from Alatalo and Alatalo (1977). We used relativized calculations (i.e. the relative number of additional species compared with data from single traps and years).

At the forest level, we compared species richness (only the 'all species' group) between two stand types A and B, estimated with one or two traps per plot. Species richness was assessed using the order-1 Chao richness estimator corrected for bias (Colwell, 1997) with 100 sample randomizations to calculate SD. The species richness difference was:

$$\text{Species richness difference} = \frac{(RS_B\text{-}RS_A)}{RS_A} \times 100 \quad (2)$$

with RS_A and RS_B being order-1 Chao estimators of the species richness in the A and B stand types, respectively. We observed whether the A-B dissimilarity values (± SD) computed for one-trap or two-trap plots overlapped.

All statistical analyses were conducted using ESTIMATES (Colwell, 1997) and R (R Development Core Team, 2010) with the lme4 (Bates *et al*., 2011), mgcv (Wood, 2008), mvtnorm (Genz *et al*., 2011), multcomp (Hothorn *et al*., 2008) and vegan (Oksanen *et al*., 2011) packages.

Results

Effects of year replication on beetle diversity assessments at trap and forest levels

The MYT trap level dataset included 517 species [417 common species (81%) and 100 rare species (19%)]. At the trap level, adding a second year of sampling gave a mean SR-Benefit value of +53% (Fig. 1) and the mean dissimilarity of assemblages

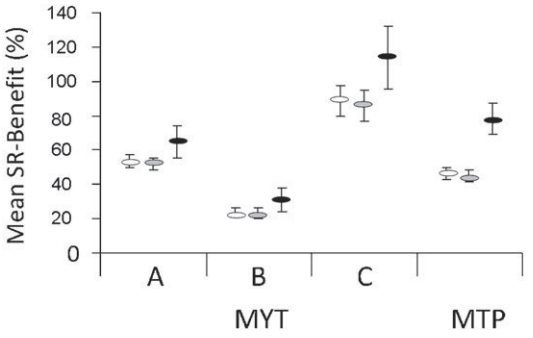


Figure 1 Mean mean benefit of species richness (SR-Benefit) values between traps (multi-trap plot; MTP) or years (multi-year trap; MYT) for 'all species', 'common species' and 'rare species'. SR-Benefit is the increase in species number caught by one supplementary trap or year, which are compared as a percentage with one single trap or one single year, respectively. In the MYT between year analyses, we tested the effects of different combinations of 1-, 2- and 3-year sampling designs on SR-Benefit: a second sampling year after the first one (SR-Benefit A), a third sampling year after two first consecutive sampling years (SR-Benefit B), two supplementary sampling years after a single first one (SR-Benefit C). Error bars represent the 95% confidence intervals.

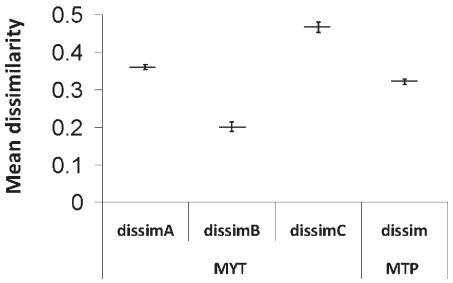


Figure 2 Mean Sörensen dissimilarity between traps (multi-trap plot; MTP) or years (multi-year trap; MYT) for 'all species'. The mean dissimilarity is the difference in species composition between assemblages caught by one single trap or one single year and assemblages caught by two traps or additional years. In the MYT between year analyses, we assessed the dissimilarity between assemblages caught with different combinations of 1-, 2- and 3-year sampling designs: a second sampling year after the first one (dissimA), a third sampling year after two first consecutive sampling years (dissimB), two supplementary sampling years after a single first one (dissimC). In the MTP between trap analyses, 'dissim' is defined as the dissimilarity between assemblages caught by one or two traps. Error bars represent the 95% confidence intervals.

between paired 1-year and 2-year designs was 36% (Fig. 2). At the forest level, using a second year of sampling increased species richness by +31%. The mean Mantel correlation between the within-site distance matrices of 1- and 2-year data was nonetheless 65%, and significant in all cases studied. Within-site between-trap distance matrices based, respectively, on 1-year or 2-year data did not differ (Table 2).

Including year-to-year variation led to notable increases in understanding of biodiversity. Overall, the number of species detected after 3 years of sampling was almost twice as large as the number of species after trapping only for 1 year (+88%) (Fig. 1). The 3-year assemblages were almost half as dissimilar as the 1-year assemblages ($D = 47\%$; Fig. 2). At the trap level, adding a third year after 2 years of sampling provided only a mean SR-Benefit value of +27% (Fig. 1). Assemblages based on 3 years of data were only 20% dissimilar to those from 2 years of collecting.

The SR-Benefit values for common species were similar to those calculated for the whole assemblage. However, these were much higher for the group of rare species only: +63% from a 1-year design to a 2-year design and even +112% from a 1-year design to a 3-year design (Fig. 1). Benefit values were much more variable for rare species only (the confidence interval was wider; Fig. 1).

At the trap level, we did not observe any effect of forest type, climatic domain, altitudinal group or baiting status on of SR-Benefit or assemblage dissimilarity in any analysis.

Effects of trap replication on beetle diversity assessments at trap and forest levels

The MTP plot level dataset included 511 species [417 common species (82%) and 94 rare species (18%)]. Using two traps/plot provided a mean SR-Benefit value of +48% compared with using one trap/plot (Fig. 1). This value was similar for analysis of common species only (+46%) but was much higher for data about rare species (+78%). Mean assemblage dissimilarity between designs with paired one-trap and two-trap plots was 33% (Fig. 2). At the forest level, two-trap plots provided 25% more species, on average, than one-trap plots. Nonetheless, the mean Mantel correlation value between the within-site distance matrices of one- and two-trap plots was 66% and was consistently significant (Table 2).

Similar to the analysis of MYTs, we did not find any relationship between SR-Benefit or assemblage dissimilarity that could be related to forest type, climatic domain or altitudinal group, or related to trap bait.

Comparative effects of trap and year replication on beetle diversity assessments at trap and forest levels

On average, sampling designs with two traps per plot or two sampling years returned more species and the effects of an additional trap or an additional year were similar (Fig. 3). The relative increase in richness as a result of trap replication exclusively was approximately 48%, whereas the increase as a result of year replication exclusively was 53%. However, the increase reflected in both approaches to replication was much lower for common species (mean of 17%). These effects were caused mostly by additions of rare species in the catches (Fig. 3); the increase as a result of the addition of a single trap was 43.8% and the increase as a result of a second year of data was similar at approximately 44.7%. By contrast to the results reported above for common species, increases in rare species were more commonly seen in both kinds of replication (40.8%) (Fig. 3). The increase was explainable by trap replication exclusively, by year replication exclusively and by both replication modes redundantly. However, the relative increase in the number of rare species was highly variable.

Effect of trap replication on ecological comparisons of stand types

In all datasets, assemblages from the stand types compared (i.e. managed/unmanaged, dead wood poor/rich, mature/overmature) were less dissimilar with two traps (mean of 68%) compared with one trap per plot (73%); however, these dissimilarity values (± SD) always overlapped. On average, over the eight cases studied, the difference in species richness between the two stand types was similar using one-trap or two-trap plots (approximately 20% as absolute values in both cases). The magnitude of this difference between two- and one-trap plots depended on the case. No significant changes in the direction (A > B or B > A) of the difference between stand types was observed using one-trap or two-trap plots. However, in terms of estimated species richness, two comparisons gave significant A−B differences with two-trap plots only (Table 4). The only significant A−B difference found with one-trap plots remained significant using data from two-trap plots.

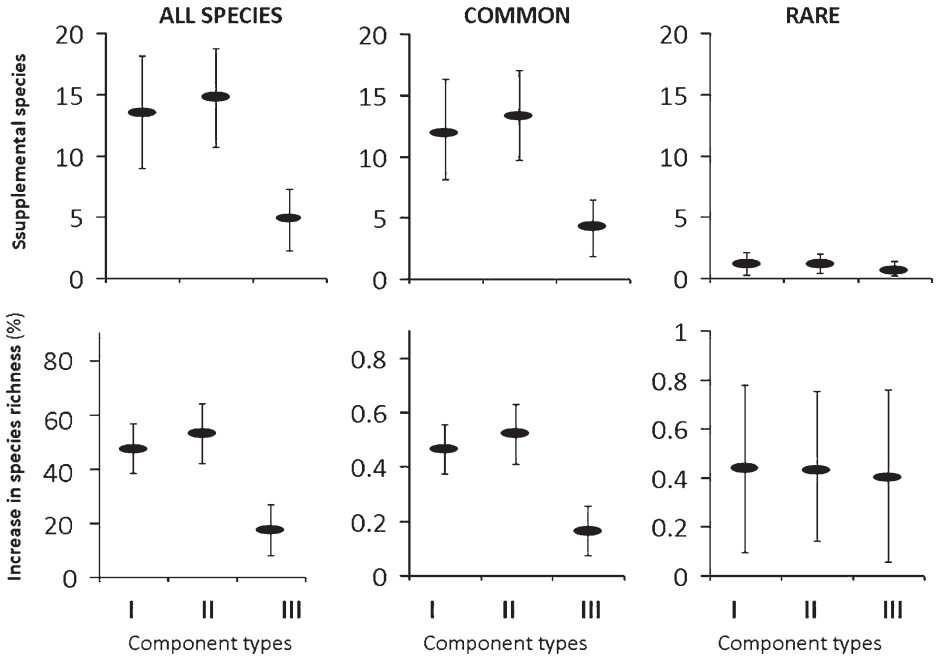


Figure 3 Exclusive and interactive effects of trap or year replication on the total species richness in two-trap and 2-year plot designs, for all, common and rare species (multi-trap-multi-year-plot; MTMYP dataset). The increase in species richness was partitioned into three components: as a result of trap replication exclusively (from one to two traps) (I), as a result of year replication exclusively (from 1 to 2 years) (II) and as a result of both replication modes redundantly (III). Error bars are the SD.

Table 4 Effects of sampling effort per plot (number of traps) on faunistic comparisons of different stand types

			Comparison between A and B stand types			
			One trap per plot		Two traps per plot	
Stand type	Forests	Number of plots (traps)	Species richness difference	Assemblage (A–B) dissimilarity(%)	Species richness difference	Assemblage (A–B) dissimilarity(%)
A = Managed	Auberive	24 (42)	10%^{NS}	71.30	13%^{NS}	65.40
B = Reserve	Fontainebleau	25 (50)	−25%^{NS}	78.80	−27%*	73.12
A = dead Wood-poor	Rambouillet	60 (120)	23%^{NS}	66.97	6%^{NS}	61.41
	Landes	52 (104)	−1%^{NS}	77.96	−30%*	73.27
B = dead Wood-rich	BelgWal Year1	22 (44)	34%^{NS}	75.28	10%^{NS}	70.33
	BelgWal Year2	22 (44)	−12%^{NS}	82.15	23%^{NS}	76.52
A = mature	Coppices	29(58)	36%*	64.73	41%*	62.79
B = overmature	Troncais-CEM	31(62)	−20%^{NS}	68.49	6%^{NS}	62.49
	Mean		|20.1%|	73	|19.5%|	68

*If order-1 Chao estimators of species richness in forest categories A and B did not overlap, not significant (NS) if they overlapped; Sörensen dissimilarity values (+/− SD) did overlap in all comparisons of forest categories A and B with 1 or 2 traps per plot. The difference in species richness (order-1 Chao estimators) was calculated as the percentage of supplementary species in the B compared with the A stand type. Mean values of species richness difference were based on absolute values (|mean value|). Plots were considered to be dead wood-rich, using the thresholds: 30 m^3/ha in the Rambouillet oak forest and in the Belgian oak-beech forests, and 20 m^3/ha in the French Landes pine forest. Mature high forests were 150–175 years old; overmature high forests were more than 200 years old (Troncais); mature coppices were 25–30 years old, whereas overmature coppices were 70–80 years old (Coppices). The number of traps between brackets is the total number of traps per site.

Discussion

Replication and species richness estimates

Adding both traps and years to studies of saproxylic beetle assemblages dramatically increased the number of beetle species collected at either the plot or forest level. On average, at the plot level, adding both an additional year and an additional trap provided a 50% increase in the number of detected species. The impact was more striking for rare species with a 75% increase in the number of species. On average, assemblages based on fewer traps and years were 35% dissimilar to those with more extensive samples. At the forest level, either year or trap replication provided a lesser increase in species richness (31% and 25%, respectively). Species detection was similarly increased by either year replication or trap replication (one to two traps).

Despite large differences in species detection, ecological studies that ask functional questions about the general effects of various treatments or management strategies may not be deeply affected, although the magnitude of differences may be considerably underestimated. However, the problem remains for those who aim to monitor biodiversity as a conservation measure. They are limited by the efficiency of sampling schemes and the extent to which possible approaches provide sufficient data (especially on rare species).

Temporal consistency and yearly variations

Our results support the findings of White *et al*. (2006) concerning the importance of considering the yearly variation in species assemblages when estimating species richness and assemblage characteristics.

Increases in species number or contrasts in assemblage composition were driven more by rare than by common species. Similarly, Martikainen and Kaila (2004) showed that rare species richness varies greatly between years and does not vary synchronously among forests. During a 10-year study, they observed a low between-year dissimilarity for common species (approximately 20–30%) but a higher between-year dissimilarity for rare species. They showed that most of the common species observed over a 10-year sampling period had already been sampled in the first 3 years. In the present study, successively adding a second or a third sampling year (compared with 1 year only) gave 50% dissimilar assemblages, twice the number of species and 112% more rare species at the trap level. Even at the forest level, a 1-year replication provided a 31% increase in species richness.

Inter-annual variation of saproxylic beetle assemblages is driven by several processes: beetle density and flight activity (Nageleisen & Bouget, 2009), meteorological variations (Williams, 1940; Rink & Sinsch, 2007), multi-year developmental cycles, variation in mean reproductive activity and the proportion of reproducing individuals driven by food availability and/or weather factors, and, finally, yearly variations in predator effects on prey populations (Turchin *et al*., 1999). These sources of variation are well appreciated for ground beetles (Klenner, 1989; Niemelä *et al*., 1992; Heyborne *et al*., 2003; Irmler, 2003; Scott & Anderson, 2003) and also for saproxylic beetles (Ranius, 2001; Martikainen & Kouki, 2003). These variations lead to a 'time-dependent species accumulation'. A multiple-year sampling strategy reduces the influence of between-year variations on data quality (Martikainen & Kaila, 2004).

Between-trap within-plot variations

Small-scale variation in microclimatic conditions, habitat and microhabitat distribution patterns among plots may lead to between-trap variation in beetle catches. The influence of small-scale heterogeneity in beetle habitats on trap catches has already been shown in pitfall trap data for carabid beetles (Niemelä *et al*., 1986; Desender & Pollet, 1988; Niemelä & Spence, 1994; Brose, 2002). The importance of the immediate surroundings on catches of freely hanging flight intercept traps has also been demonstrated (Sverdrup-Thygeson & Birkemoe, 2008). Our data showed significant assemblage dissimilarity between catches of two traps located only approximately 20 m apart in the same stand. The results obtained in the present study therefore strengthen the hypothesis that finescale patterns of habitat structure could play an important role in trap catches. Although traps may be located close together, data will differ depending on whether or not they are in flight corridors, near rich microhabitats, or in open or closed spots.

At a larger spatial scale (i.e. a forest), the SR-Benefit associated with trap replication appears to decrease; its value at the forest level is halved compared with the value at the local plot level (site = 25%; plot = 50%). Nonetheless, the results of research projects at the forest level may be affected to some extent by trap replication. For example, trap replication strengthened some previously insignificant trends in the present study. Simply doubling the number traps per plot changed the results for ecological comparisons of species richness in 25% of the cases studied. However, the comparison of assemblages in the selected stand types did not differ significantly among one-trap or two-trap plots.

Sampling rare species

Sampling rare species is especially challenging because they represent only a small part of the total number of species caught (McArdle, 1990), approximately 20% in our data. Unlike some studies (Niemelä *et al*., 1990; Novotny & Basset, 2000; Grove, 2002b) that define rare species as those poorly represented in their samples, we followed Martikainen and Kaila (2004) and *a priori* defined as rare those species listed as such in reliable databases (i.e. the French FRISBEE database in our case; Bouget *et al*., 2008).

For the results obtained in the present study, at the plot level, all SR-Benefits associated with year replication were significantly higher for rare than for common species. Moreover, the annual SR-Benefit remained high (+73% of rare species from 1- to 2-year replicates, +38% of rare species from 2- to 3-year replicates) throughout a 3-year sampling period. Furthermore, Martikainen and Kaila (2004) demonstrated that the annual number of detected rare species is constant throughout a 10-year sampling period. A multi-year study would therefore be particularly valuable to detect a large amount of rare species. Martikainen and Kouki (2003) and Martikainen and Kaila (2004) observed that catches of rare species in small samples are random and that between-site comparisons based on such limited data do not provide very useful results.

In the present study, year or trap replication provided an equivalent +75% increase in the number of detected rare species at the plot level. Hedgren and Weslien (2008) showed that selective trap placement (near well-known rich microhabitats) was a more efficient way of catching rare species than random trap placement. In the data obtained in the present study, even if adding a second trap per plot is assumed to sample a wider range of microhabitats at the plot scale, the relative and net increase in rare species detection with an additional trap was not higher than that with an additional sampling year. Data from a second sampling year accounts for between-year variation in rare beetle species density and activity.

Practical recommendations for saproxylic beetle diversity surveys

Given the high between-trap variation in species number and composition within plots, we recommend that ecological comparisons in species richness should be made at the plot level and not at the trap level.

Our efforts to partition the effects on increase in species richness suggest that an extra trap had a similar effect to an extra year. However, yearly replication will accommodate mainly inter-annual variation in species occurrences, and trap replication will probably accommodate microhabitat variation (Hedgren & Weslien, 2008). In our analysis, the additional species differed between spatial and temporal replication modes. For common species, the gross effect of sampling replication (both trap and year) was significantly lower than the trap or the year replication effect. In other words, the specific effect on catches of either yearly variation or small-scale habitat heterogeneity was stronger than a raw replication effect (whatever the mode). For rare species, however, the interactive effect of trap and year replication on the increase in species richness was as important as the exclusive effects of trap or year replication. As previously suggested by Martikainen and Kaila (2004), the raw effect of replication therefore appears to be more important for rare species.

A complete comparison of relative benefits of these two replication approaches should take costs into account. On average, field work accounts for only 20% of the working time for data collection in a monitoring or research programme, whereas the remaining 80% is sorting and identification work in the laboratory (Bouget, 2009). However, this feature depends strongly on the spatial extent of the programme because field costs indeed grow higher as the spatial scale of programmes increases. Thus, trap replication is recommended in large-scale programmes, mainly for economic reasons. The required sampling strategy should obviously take into account space and time constraints dependent on the objectives of the sampling programme (analysis of environment–biodiversity relationships, long-term monitoring, intensive inventory, etc.).

Power analyses are needed to better define the minimum number of traps per plot required to be able to detect at least 5% differences between two groups of plots. Similarly, at the forest level, it would be useful to better understand the minimum number of plots required to compare two groups of sites. To detect most common species in a site, Martikainen and Kaila (2004) suggested using at least 20 traps during one single year. Plots containing a larger number of traps are required to properly study the sample-dependent species accumulation rate.

Conclusions and perspectives

Our analyses were based on existing data obtained from France and Belgium after compiling them in a way that permitted comparison. Significant benefits of replication were demonstrated despite a narrow range of year or trap replication. Slight variation in sampling effort (adding trap or year) deeply affected the quality of data.

Further studies about the relationships between sampling effort and catch characteristics based on a broader range of raw data (longer time series, denser sampling plots) will be useful for suggesting practical guidelines with respect to the sampling strategies used in monitoring schemes. A longer time frame for studies explicitly designed to support this type of analysis would facilitate the better analysis of time-dependent species accumulation rates. In addition, long-term studies would allow us to better understand inter-annual fluctuations in assemblage composition (Kozlov *et al*., 2010) and the impacts of global patterns of increasing or decreasing populations (Conrad *et al*., 2004; Salama *et al*., 2007), especially under the influence of climate change.

Unfortunately, long-term, large-scale intensive insect sampling designs are scarce despite their obvious relevance to effective biological conservation and efficient biodiversity monitoring. The collection of such data is currently limited by financial constraints, a lack of qualified personnel or by institutional changes in research orientations (Jackson & Füreder, 2006). We hope that the findings of the present study, aiming to better understand the sampling methods for saproxylic beetles, provide or improve existing tools and aid in the design of cost-effective biodiversity monitoring schemes.

Acknowledgements

We thank Frederic Gosselin for his help with the data analysis and for helpful comments on the first drafts of the paper; Pavel Sebek for his contribution to the data compiling; and Bruno Meriguet, Olivier Rose, Thomas Barnouin, Fabien Soldati, Hervé Brustel, Thierry Noblecourt, Lionel Valladares, Benoit Nusillard and Carl Moliard for help with data collection. We are indebted to John Spence and two anonymous rewiers for their useful comments on an earlier version of the manuscript. We also thank Vicki Moore for checking and improving our written English.

References

Alatalo, R.V. & Alatalo, R.H. (1977) Components of diversity: multivariate analysis with interaction. *Ecology*, **58**, 900–906.

Alexander, K. (2008) Tree biology and saproxylic coleoptera: issues of definitions and conservation language. *Revue d'Ecologie (Terre Vie)*, **63**, 1–7.

Alinvi, O., Ball, J.P., Danell, K., Hjältén, J. & Pettersson, R.B. (2006) Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. *Journal of Insect Conservation*, **11**, 99–112.

Bates, D., Maechler, M. & Bolker, B. (2011) *lme4: Linear Mixed-effects Models Using S4 Classes*. R package version 0.999375-39 [WWW document]. URL http://CRAN.R-project.org/package=lme4 [accessed on 1 February 2012].

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.

Bouget, C. (2009) Levels of taxonomic resolution in forest entomology studies: needs, contingencies and perspectives. *Mémoires de la Société Entomologique de France*, **8**, 75–80 (in French).

Bouget, C. & Brustel, H. (2009) Chapter 4: target insect groupes in temperate forests, II – Saproxylic Coleoptera. *Forest Insect Studies: Methods and Techniques. Key Considerations for Standardisation. An*

Overview of the Reflections of the 'Entomological Forest Inventories' Working Group (Inv.Ent.For). Vol. 19: Les Dossiers Forestiers (ed. by L. M. Nageleisen and C. Bouget), pp. 100–111. Office National des Forêts, France.

Bouget, C., Brustel, H. & Zagatti, P. (2008) The French information system on saproxylic beetle ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation status. *Revue d'Ecologie (suite de La Terre et la Vie)*, **10** (Suppl), 33–36 [WWW document]. URL http://frisbee.nogent.cemagref.fr/index.php/en [accessed on 1 February 2012].

Brose, U. (2002) Estimating species richness of pitfall catches by non-parametric estimators. *Pedobiologia*, **46**, 101–107.

Brustel, H. (2001) *Coléoptères saproxyliques et valeur biologique des forêts françaises*. PhD Dissertation, University of Toulouse, Institut National Polytechnique.

Brustel, H. (2004) 'Polytrap™' a window flight trap for saproxylic beetles. *Third Symposium and Workshop on the Conservation of Saproxylic Beetles*, Lativa.

Colwell, R.K. (1997) *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 8. User's Guide and Application*. University of Connecticut, Storrs, Connecticut [WWW document]. URL http://viceroy.eeb.uconn.edu/EstimateS [accessed on 1 February 2012].

Comité des Ministres (1988a) *Recommandation N° R (88) 10 du Comité des Ministres aux états membres pour la conservation des organismes saproxyliques et leurs biotopes (adoptée par le Comité des Ministres le 13 juin 1988, lors de la 418e réunion des Délégués des Ministres)*.

Comité des Ministres (1988b) *Recommandation N° R (88) 11 du Comité des Ministres aux états membres pour la conservation des organismes saproxyliques et leurs biotopes (adoptée par le Comité des Ministres le 13 juin 1988 lors de la 418e réunion des Délégués des Ministres)*.

Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R. & Warren, M.S. (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation*, **8**, 119–136.

Desender, K. & Pollet, M. (1988) Sampling pasture carabids with pitfalls: evaluation of species richness and precision. *Mededelingen van de Faculteit Landbouwwetenschappen van de Rijksuniversiteit Gent*, **53**, 1109–1117.

Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C. & Lambin, X. (2001) Analysis of aggregation, a worked example: numbers of ticks on red grouse chick. *Parasitology*, **122**, 563–569.

ETCB (European Topic Centre on Biological Diversity) (2006) *The Indicative Map of European Biogeographical Regions: Methodology and Development*. Muséum National d'Histoire Naturelle, France.

Genz, A., Bretz, F., Miwa, T., Mi, X., Leisch, F., Scheipl, F. & Hothorn, T. (2011) *mvtnorm: Multivariate Normal and t Distributions*. R Package Version 0.9-96 [WWW document]. URL http://CRAN.R-project.org/package=mvtnorm [accessed on 1 February 2012].

Grove, S.J. (2002a) Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, **33**, 1–23.

Grove, S.J. (2002b) The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biological Conservation*, **104**, 149–171.

Hammond, J.H.E., Langor, D.W. & Spence, J.R. (2004) Saproxylic beetles (Coleoptera) using Populus in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. *Canadian Journal of Forest Research*, **34**, 1–19.

Hedgren, O. & Weslien, J. (2008) Detecting rare species with random or subjective sampling: a case study of red-listed saproxylic beetles in boreal Sweden. *Conservation Biology*, **22**, 212–215.

Heyborne, W.H., Miller, J.C. & Parsons, G.L. (2003) Ground dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA. *Forest Ecology and Management*, **179**, 123–134.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.

Hyvärinen, E., Kouki, J. & Martikainen, P. (2006) A comparison of three trapping methods used to survey forest-dwelling Coleoptera. *Eurasian Journal of Entomology*, **103**, 397–407.

Irmler, U. (2003) The spatial and temporal pattern of carabid beetles on arable fields in northern Germany (Schleswig-Holstein) and their value as ecological indicators. *Agriculture, Ecosystems and Environment*, **98**, 141–151.

Jackson, J.K. & Füreder, L. (2006) Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. *Freshwater Biology*, **51**, 591–603.

Klenner, M. (1989) Überlebenstrategien einer stenotopen Waldart : Untersuchungen zur Dynalik einer westfälischen *Carabus auronitens* Population (Coleoptera, Carabidae). *Verhandlungen der Gesellschaft für Ökologie*, **18**, 781–791.

Kozlov, M.V., Hunter, M.D., Koponen, S., Kouki, J., Niemelä, J. & Price, P.W. (2010) Diverse population trajectories among coexisting species of subarctic forest moths. *Population Ecology*, **52**, 295–305.

Lachat, T., Nagel, P., Cakpo, Y., Attignon, S., Goergen, G., Sinsin, B. & Peveling, R. (2006) Dead wood and saproxylic beetle assemblages in a semi-deciduous forest in Southern Benin. *Forest Ecology and Management*, **225**, 27–38.

Martikainen, P. & Kaila, L. (2004) Sampling saproxylic beetles: lessons from a 10-year monitoring study. *Biological Conservation*, **120**, 175–185.

Martikainen, P. & Kouki, J. (2003) Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodiversity and Conservation*, **12**, 1815–1831.

McArdle, B.A. (1990) When are rare species not there? *Oikos*, **57**, 276–277.

McIntosh, R.L., Katinic, P.J., Allison, J.D., Borde, J.H. & Downey, D.L. (2001) Comparative efficacy of five types of trap for woodborers in the Cerambycidae, Buprestidae and Siricidae. *Agricultural and Forest Entomology*, **3**, 113–120.

Nageleisen, L.M. & Bouget, C. (2009) *Forest Insect Studies: Methods and Techniques. Key Considerations for Standardisation. An Overview of the Reflexions of the 'Entomological Forest Inventories' Working Group (Inv.Ent.For). Les dossiers forestiers n°19*. Office National des Forêts, France.

Niemelä, J.K. & Spence, J.R. (1994) Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography*, **17**, 166–175.

Niemelä, J., Halme, E., Pajunen, T. & Haila, Y. (1986) Sampling spiders and carabid beetles with pitfall traps: the effect of increased sampling effort. *Annales Entomologici Fennici*, **52**, 109–111.

Niemelä, J., Halme, E. & Haila, Y. (1990) Balancing sampling effort in pitfall trapping of carabid beetles. *Entomologica Fennica*, **1**, 233–238.

Niemelä, J., Spence, J.R. & Spence, D.H. (1992) Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Canadian Entomologist*, **124**, 521–540.

Nieto, A. & Alexander, K.N.A. (2010) *European Red List of Saproxylic Beetles*. Publications Office of the European Union, Luxembourg.

Novotny, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, **89**, 564–572.

Ohsawa, M. (2007) The role of isolated old oak trees in maintaining beetle diversity within larch plantations in the central mountainous region of Japan. *Forest Ecology and Management*, **250**, 215–226.

Økland, B. (1996) A comparison of three methods of trapping saproxylic beetles. *Eurasian Journal of Entomology*, **9**, 195–209.

Oksanen, J., Blanchet, F.G., Kindt, R. *et al*. (2011) *vegan: Community Ecology Package*. R Package Version 2.0-2 [WWW document]. URL

http://CRAN.R-project.org/package=vegan [accessed on 1 February 2012].

Ranius, T. (2001) Constancy and asynchrony of *Osmoderma eremita* populations in tree hollows. *Oecologia*, **126**, 208–215.

R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria. [WWW document]. URL http://www.R-project.org [accessed on 1 February 2012].

Rink, M. & Sinsch, U. (2007) Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. *Journal of Zoology*, **272**, 235–243.

Salama, N.K.G., Knowler, J.T. & Adams, C.E. (2007) Increasing abundance and diversity in the moth assemblage of east Loch Lomondside, Scotland over a 35 year period. *Journal of Insect Conservation*, **11**, 151–156.

Scott, W.A. & Anderson, R. (2003) Temporal and spatial variation in carabid assemblages from the United Kingdom Environmental Change Network. *Biological Conservation*, **110**, 197–210.

Siitonen, J. (1994) Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. *Annales Zoologici Fennici*, **31**, 89–95.

Stokland, J., Tomter, S. & Söderberg, U. (2004) Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. *Monitoring and Indicators of Forest Biodiversity in Europe – From Ideas to Operationality, EFI Workshop, 12–15 November 2003, Italy* (ed. by M. Marchetti), pp. 207–226. European Forest Institute, Finland.

Sverdrup-Thygeson, A. & Birkemoe, T. (2008) What window traps can tell us: effect of placement, forest openness and beetle reproduction in retention trees. *Journal of Insect Conservation*, **13**, 183–191.

Turchin, P., Taylor, A.D. & Reeve, J.D. (1999) Population cycles of a forest insect: an experimental test. *Science*, **285**, 1068–1071.

White, E.P., Adler, P.B., Lauenroth, W.K., *et al*. (2006) A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos*, **112**, 185–195.

Wikars, L.O., Sahlin, E. & Ranius, T. (2005) A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *Canadian Entomologist*, **137**, 304–324.

Williams, C. (1940) An analysis of four years captures of insects in a light trap. Part 2. The effect of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population. *Transactions of the Royal Entomological Society of London*, **90**, 227–306.

Wood, S.N. (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society B*, **70**, 495–518.

Accepted 22 December 2012
First published online 1 March 2013

Article 2: Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests?

Bulletin of Entomological Research (2015) **105**, 101–109 doi:10.1017/S0007485314000741

Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests?

G. Parmain[1,2,3]*, C. Bouget[1], J. Müller[4], J. Horak[5], M.M. Gossner[6], T. Lachat[7] and G. Isacsson[8]

[1]National Research Institute of Science and Technology for Environment and Agriculture. (IRSTEA), 'Forest ecosystems' Research Unit, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France: [2]National Laboratory of Forest Entomology, National Forest Office (ONF), F-11500 Quillan, France: [3]National Museum of Natural History, Natural Patrimony Department, 36 rue Geoffroy St Hilaire, CP 41 75 231 Paris cedex 05, France: [4]Nationalparkverwaltung Bayerischer Wald Stellvertretender Leiter Sachgebietsleiter Naturschutz und Forschung Freyunger Str. 2, 94481 Grafenau, Germany: [5]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamycka 1176, CZ-165 21 Prague, Czech Republic: [6]Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising-Weihenstephan, Germany: [7]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland: [8]Swedish Forest Agency, P.O. Box 63, SE-281 21 Hässleholm, Sweden

Abstract

Monitoring saproxylic beetle diversity, though challenging, can help identifying relevant conservation sites or key drivers of forest biodiversity, and assessing the impact of forestry practices on biodiversity. Unfortunately, monitoring species assemblages is costly, mainly due to the time spent on identification. Excluding families which are rich in specimens and species but are difficult to identify is a frequent procedure used in ecological entomology to reduce the identification cost. The Staphylinidae (rove beetle) family is both one of the most frequently excluded and one of the most species-rich saproxylic beetle families. Using a large-scale beetle and environmental dataset from 238 beech stands across Europe, we evaluated the effects of staphylinid exclusion on results in ecological forest studies. Simplified staphylinid-excluded assemblages were found to be relevant surrogates for whole assemblages. The species richness and composition of saproxylic beetle assemblages both with and without staphylinids responded congruently to landscape, climatic and stand gradients, even when the assemblages included a high proportion of staphylinid species. At both local and regional scales, the species richness as well as the species composition of staphylinid-included and staphylinid-excluded assemblages were highly positively correlated. Ranking of sites according to their

*Author for correspondence
Phone: 00.33.2.38.95.66.78
Fax: 00.33.2.38.95.03.59
E-mail: guilhem.parmain@irstea.fr

biodiversity level, which either included or excluded Staphylinidae in species richness, also gave congruent results. From our results, species assemblages omitting staphylinids can be taken as efficient surrogates for complete assemblages in large scale biodiversity monitoring studies.

Keywords: biodiversity surrogate, insect sampling, biodiversity monitoring, identification cost

(Accepted 19 September 2014)

Introduction

The importance of beech forests for forest biodiversity conservation in Central Europe has recently been highlighted by several studies (Müller *et al.*, 2013; Lachat *et al.*, 2012; Gossner *et al.*, 2013). Within beech forest biodiversity, deadwood-associated (saproxylic) species account for about 25% of the total species richness occurring in temperate and boreal forest ecosystems (Siitonen, 2001; Stokland *et al.*, 2004). This high proportion makes them challenging candidates for forest biodiversity monitoring. However, the species-rich saproxylic group is often seen as a response group in forest ecology. Furthermore, this group is known to be highly sensitive to forest management and has consequently become threatened (Nieto & Alexander, 2010). Furthermore, saproxylic organisms may be used to discriminate old-growth forests from managed ones (Siitonen & Saaristo, 2000), or as indicators for different forestry regimes (Davies *et al.*, 2008).

Among the saproxylic organisms, beetles account for more than 20% of the species diversity (Stokland *et al.*, 2004) and are often used as a relevant indicators of forest management impacts for convenience and practical reasons. Monitoring saproxylic beetle diversity has three main objectives: (i) forest site ranking, i.e., sorting sites according to their biodiversity level, and to identify relevant conservation sites (Timonen *et al.*, 2010), (ii) identifying environmental structural drivers of forest biodiversity (Bouget *et al.*, 2014) in order to establish efficient conservation measures and management guidelines, and (iii) assessing the impacts of forest management on biodiversity (Davies *et al.*, 2008).

The monitoring of species assemblages is nonetheless costly, mainly due to difficult and time-consuming species identification (Müller & Brandl, 2009). High resolution analyses require informative long-time and costly datasets. The importance of data quality in saproxylic ecological studies has already been highlighted (Parmain *et al.*, 2013). Several strategies are available to simplify the study of saproxylic species assemblages, especially to reduce the time spent on identification. These strategies imply the identification of specimens (i) at a morphospecies level (Obrist & Duelli, 2010), (ii) a supra-species level (e.g., genus level), or (iii) at the species level for only a species subset (indicators – Schmidl & Bussler, 2004) or selected families or species (monitoring species – Müller & Gossner, 2010).

Morphospecies, instead of species, have been used in order to reduce identification cost, but this seems more efficient for butterflies and spiders (Derraik *et al.*, 2002) than for beetles (Olivier & Beattie, 1996). Supra-species monitoring, also called 'taxonomy sufficiency', is widely used to rapidly assess changes in biodiversity (Beattie & Olivier, 1994), but it does not allow researchers to determine fine-scale changes (Williams & Gaston, 1994) nor can multivariate analyses be computed (Terlizzi *et al.*, 2003). Species subsets may be easier, cheaper and faster to study than the entire target group (Williams & Gaston, 1994), but relevant subsets able to predict overall species richness are difficult to identify. Within the saproxylic beetle group, the explanatory power of several species subsets have already been tested, such as easy-to-identify (Sebek *et al.*, 2012) or red-listed species (Timonen *et al.*, 2010; Lachat *et al.*, 2012). A near-full set of species can be quickly obtained while excluding the families whose identification is very time-consuming or taxonomically complicated (Kennedy & Jacoby, 1997). Family exclusion is therefore a frequently used procedure in beetle studies (Grove, 2002; Ohsawa, 2007; Bouget *et al.*, 2014). Most of the excluded families are taxonomically complicated and their biology is not well known. Among saproxylic beetle families, some are nearly always kept for analyses (Cerambycidae, Elateridae, Cetoniidae) whereas others are often excluded from mass-trapping samples to exclude doubtful data (*Cryptophagus* and *Atomaria* genera in Cryptophagidae, *Epuraea* in Nitidulidae, Latridiidae and Staphylinidae, especially Aleocharinae). Sebek *et al.* (2012) explored the surrogate ability of several saproxylic beetle families, either individually or in combination, to estimate total species richness per trap. However, rove beetles (Staphylinidae) were not available in the beetle dataset they used.

The rove beetle family is one of the most species-rich saproxylic beetle families (just behind longhorn beetles. Supplementary Material). Today, staphylinid taxonomy is in effervescence worldwide, with many new species being described (Brunke *et al.*, 2012). On the other hand, it is also one of the most frequently excluded taxa. In some forest environments, staphylinids are one of the most abundant and species-rich families in trapped saproxylic beetle assemblages (Alinvi *et al.*, 2007; Müller *et al.*, 2008). In addition to their hyper-diversity (they are the most species-rich saproxylic subfamily in western Europe), Staphylinidae are hard to identify for the following reasons: (i) there are very few specialized taxonomical experts (Kim & Byrne, 2006); (ii) identification keys and books are difficult to keep up to date due to the quickly evolving taxonomy (though recent publications (Löbl & Smetana, 2004; Assing & Schülke, 2011) have updated the previous identification tools (Lohse, 1964; Lohse *et al.*, 1974) for Central Europe (excluding, however, some species-rich sub-families such as Aleocharinae, Pselaphinae and Scydmaeninae); (iii) identification requires the analysis of internal genitalia, i.e., the Aleocharinae, (Schmidl & Bussler, 2004; Bouget *et al.*, 2008; Stokland & Meyke, 2008); and (iv) the few specialists are rapidly overwhelmed by the huge quantities of samples related to large-scale sampling designs (Langor *et al.*, 2006).

These reasons all indicate that excluding Staphylinidae from forest biodiversity samples may save time and money

Table 1. Description of variables (macro-climate, stand, region and landscape) explored in the study. See Gossner *et al.* (2013) for further details.

			Min	Mean (SD)	Max
Climatic	bio_10	Mean temperature of warmest quarter	116.5	158.1 (10.80)	184.7
	bio_18	Precipitation of the warmest quarter	165.8	310.4 (65.48)	434.4
Landscape	Deciduous3000 m	On a 3 km radius around the center of each stand: proportion of deciduous forest	0.005	0.4205 (0.233)	1
	Conifer3000 m	On a 3 km radius around the center of each stand: proportion of conifer forest	0	0.1931 (0.187)	0.74
	Urban3000 m	On a 3 km radius around the center of each stand: proportion of traffic and settlements	0	0.03 (0.049)	0.31
Region	1	Belgium, North-western Germany, Luxembourg		$n=512$	
	2	Western Germany, Switzerland		$n=205$	
	3	Sweden		$n=70$	
	4	Czech Republic, Slovakia		$n=50$	
	5	Czech Republic, Southern Germany		$n=164$	
	6	Germany		$n=95$	
	7	Italy		$n=83$	
	8	Ukraine		$n=9$	
Stand	Deadwood amount	Dead wood volume estimation in a 25 m radius around the trap.		Low ($<30\,m^3\,ha^{-1}$; $N=689$), medium ($30–70\,m^3\,ha^{-1}$; $N=257$), high ($>70\,m^3\,ha^{-1}$; $N=242$)	
	Protection	Considered unmanaged only if no harvesting had occurred for at least 10 years		N unmanaged = 339 N managed = 849	
	Veteran tree	Presence of veteran tree in the surroundings of the trap. Veteran trees have a DBH > 70		N presence = 447; N absence = 741	
	Elevation	Altitude of the stand		Plain $N=404$, Hill $N=608$ and Mountain $N=176$	
Bio-region		Alpine		$n=103$	
		Atlantic		$n=14$	
		Continental		$n=1062$	
		Mediterranean		$n=9$	

and make saproxylic beetle datasets more rapidly available for analysis. Nonetheless, the effects of such an exclusion on the results in ecological studies must be evaluated.

Using a large-scale dataset compiled in European beech forests (Müller *et al.*, 2013), we addressed the following main questions:

Do saproxylic beetle assemblages with and without staphylinids congruently respond to ecological (landscape, macroclimatic and local) gradients? How do the species richness and composition of assemblages with and without staphylinids co-vary?

In addition, we analyzed this secondary issue:

Is the response of staphylinid-restricted assemblages to ecological gradients well reflected by the response of staphylinid-excluded assemblages?

Material and methods

We compiled saproxylic beetle data obtained during various projects and corresponding to a total of 1188 flight-interception traps in 238 forest stands dominated by European Beech (>50% beech cover) on 85 sites in nine different countries (see Supplementary Material) from Sweden to Switzerland and the Ukraine (Carpathians). All traps were cross-vane flight-interception traps made up of transparent plastic windows, with total interception area comprised between 0.6 and 1 m^2.

Ecological gradients and environmental data

For the purpose of this study, forest conditions were surveyed at the following levels (see Gossner *et al.*, 2013, for details):

(i) Landscape characteristics (see table 1) (3-km radius around the center of each stand) were assessed according to the European-wide land-cover mapping project CORINE (http://www.corine.dfd.dlr.de), which uses satellite remote-sensing images at a scale of 1:100,000. Land-use information includes 44 categories, which were used to calculate the following variables (table 1): the *proportion of deciduous forest*, the *proportion of conifer stands* relative to the extent of forest and the *proportion of traffic and settlements*. For Switzerland, the variables were taken from www.swisstopo.admin.ch; for Ukraine, the variables were estimated from Google Earth aerial photos.

(ii) Climate variables (see table 1) were extracted from the WorldClim database with a resolution of 30 s and calculated as a mean value within a 1-km radius; a larger radius would have led to inaccurate values for sites in rough terrain (Hijmans *et al.*, 2005). We selected *mean temperature* and *precipitation of warmest quarter* as ecologically meaningful variables for the life cycle of beetles. In addition, we included trap *elevation*.

(iii) Stand conditions (see table 1) were defined according to three parameters: the estimated *deadwood amount* in three levels (low ($<30\,m^3\,ha^{-1}$; $N=689$), medium ($30–70\,m^3\,ha^{-1}$; $N=257$), high ($>70\,m^3\,ha^{-1}$; $N=242$)),

the *protection status* (managed versus unmanaged; a stand was considered unmanaged only if harvesting had been absent for at least 10 years), and the occurrence of *veteran trees* in the trap surroundings (presence versus absence).

Beetle data

Beetles were identified to the species level by taxonomic experts, and only saproxylic species were considered for our analyses. We classified beetles as saproxylic following Schmidl & Bussler (2004) and Köhler (2010).

We defined three types of species assemblage: (i) with Staphylinidae only (staphylinid-restricted), (ii) with all species except for Staphylinidae (staphylinid-excluded), and (iii) with all species including Staphylinidae (staphylinid-included).

We distinguished three levels of Staphylinidae species richness per trap: low (staphylinid species accounted for <10% of total trap richness; $N = 466$)), medium (staphylinid richness = 10–25% of total richness; $N = 521$)) and high (>25% of the species were Staphylinidae, $N = 201$).

Analyses

Most analyses were carried out at the trap level. The European dataset was divided into eight regions, defined by hierarchical cluster analysis (HCA) of between-trap Euclidian distance matrices between geographical coordinates (vegdist function, lme4 package (Bates *et al.*, 2014)) (Supplementary Material). These geographical clusters were included in our models as random spatial effects.

The correlations between staphylinid-restricted/staphylinid-excluded and staphylinid-included/staphylinid-excluded species richness were calculated with Spearman correlation tests.

We also analyzed the effects of staphylinid exclusion on site ranking, based on species richness. We ranked forest sites (regional scale) and stands (local scale) according to the species richness of staphylinid-included or staphylinid-excluded assemblages. We used the 'min' method in the *rank* R function to manage ties (*ex-aequos*). At both spatial scales (forest $n = 85$ and stand $n = 238$), we computed the mean absolute value of rank differences (standardized by sample size) and the total percentage of congruent rankings (±5% ranking error). After ranking, we also quantified how much the top-ten forests (or sites, or stands) diverge using staphylinidae-excluded or -included species richness values.

Contributions of environmental variables (climate, landscape and stand variables; table 1) to variations in species richness (rarefied by abundance) between staphylinid-restricted/staphylinid-excluded and staphylinid-included/staphylinid-excluded assemblages were analyzed in Linear Mixed Models, with country, forest site and stand as spatially-implicit random effects on the intercept (glmer function in lme4 (Bates *et al.*, 2014)).

Compositional differences between staphylinid-restricted/staphylinid-excluded and staphylinid-included/staphylinid-excluded assemblages were analyzed using spatially-constrained Mantel tests (method = 'pearson', permutation = 999, strata = region). To rank the effect of several variables on variations in species composition (including singletons), we performed a canonical analysis of principal coordinates (CAP) (vegan R-package, Anderson & Willis, 2003) with 'forest' as a constrained factor. Based on Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, since co-linearity among predictor variables is not considered to be a problem in CAP. We calculated the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance (permutation tests – 199 runs), and the relative contribution of each set of variables to marginal inertia.

All analyses were conducted with R 3.0.1 (R Core Team, 2013).

Results

Our compiled dataset included 552,651 individuals and 936 saproxylic beetle species. Staphylinidae was the most species-rich family (145 species). These 145 staphylinid species account for about 16% of the cumulated richness and 14% of the mean richness per trap. The contribution of rove beetles to the mean species richness per trap was not different in managed or in unmanaged stands, in deciduous- or in conifer-dominated forests, in deadwood-poor or in deadwood-rich stands, and in lowland or in mountain forests (for details, see Supplementary Material).

(1) Staphylinid-included versus staphylinid-excluded assemblages

Alpha diversity and stand ranking

At the stand level, the Spearman correlation value between species richness in staphylinid-included versus staphylinid-excluded assemblages was very high (rho = 0.99; fig. 1a). The ten most species-rich stands were consistent between staphylinid-included and staphylinid-excluded assemblages for nine out of ten stands. The stand ranking based on staphylinid-excluded data gave a similar result compared with staphylinid-included data in more than 75% of the cases, considering a 5% ranking error; respectively 77 and 79% of the cases in managed and unmanaged stands. The mean value of rank difference between staphylinid-included and staphylinid-excluded ranking standardized by sample size was 0.03, both in managed and unmanaged stands. The Mantel correlation value between staphylinid-included and staphylinid-excluded dissimilarity matrices was high and significant ($r = 0.98$, $P < 0.001$; fig. 1b).

Gamma diversity and site ranking

At the forest site level, species richness in staphylinid-included and staphylinid-excluded assemblages was strongly correlated (Spearman rho = 0.99; fig. 1c). The identification of the ten most species-rich sites in our dataset was similar with staphylinid-excluded data compared with staphylinid-included data in more than 75% of the cases (with an accepted 5% ranking error). In the Top10 sites given by the ranking of staphylinid-excluded assemblages, eight were also among the Top10 based on staphylinid-included data. The mean value of rank difference between staphylinid-included and staphylinid-excluded data ranking, standardized by sample size, was 0.03.

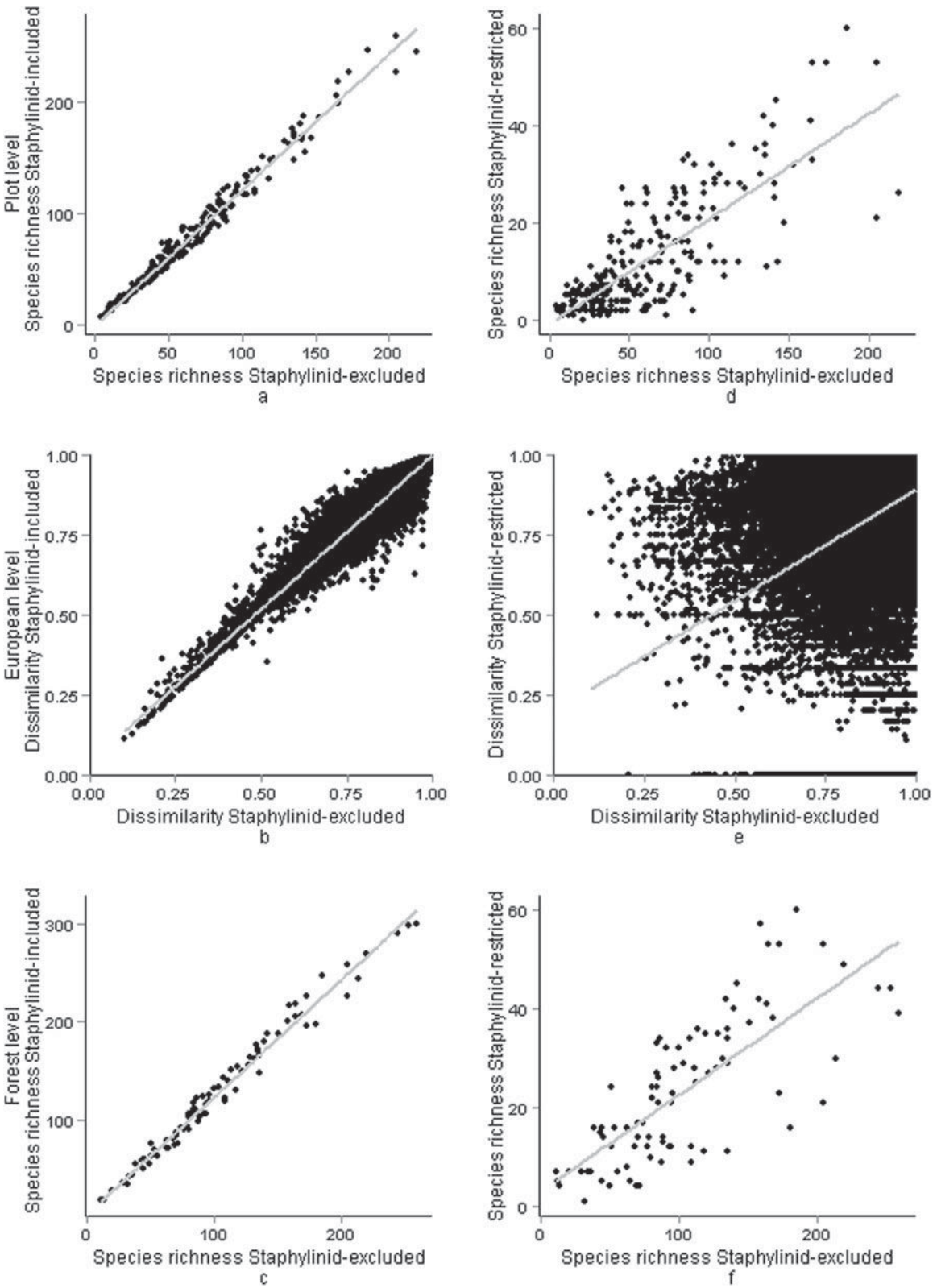


Fig. 1. a; b; c: correlation between staphylinid-included and staphylinid-excluded data. d; e; f: correlations between staphylinid-restricted and staphylinid-excluded data.

Table 2. Response in species richness of staphylinid-included, staphylinid-excluded and staphylinid-restricted assemblages to macro-climate, stand and landscape variables, analyzed using a Generalized Linear Mixed Model with a Gaussian error distribution, and forest site and stand as spatial random effects.

Trap subsets	Species assemblages	*N*traps	Deadwood amount	Elevation	Protection	Veteran trees	bio_10	bio_18	Deciduous3000 m	Conifer3000 m	Urban3000 m
All	Staphylinid-included		**	***			**	***			
	Staphylinid-excluded	1188	**	***			**	***			
	Staphylinid-restricted			***				***			
Low contribution of rove beetles to total richness (0/10%)	Staphylinid-included										
	Staphylinid-excluded	466									
	Staphylinid-restricted										
Medium contribution of rove beetles to total richness (10/25%)	Staphylinid-included		**	***			**	***			
	Staphylinid-excluded	521	**	***			**	***			
	Staphylinid-restricted		**	***				***			
High contribution of rove beetles to total richness (more than 25%)	Staphylinid-included			***							
	Staphylinid-excluded	201		***			**	**			
	Staphylinid-restricted			***				**			

Only significant responses were displayed (***$P<0.001$, ** $0.01>P>0.001$, * $0.05>P>0.01$). bio_10, mean temperature of the warmest quarter; bio_18, precipitation of the warmest quarter; Deciduous3000 m, proportion of deciduous forest in a 3 km-radius buffer; Conifer3000 m, proportion of conifer forest in a 3 km-radius buffer; Urban3000 m, proportion of traffic and settlements in a 3 km-radius buffer; Ntraps, number of traps in each Trap subset.

Environmental drivers of variations in species richness

Whether staphylinid-included or -excluded datasets were used, the influence of structural variables on species richness was consistent. Furthermore, the proportion of variance explained by fixed factors (for significant factors only, R^2) was slightly higher for staphylinid-excluded data (Supplementary Material). The level of staphylinid richness per trap did slightly influence the response of beetle species richness to environmental parameters. In the dataset restricted to traps with low or medium staphylinid richness, the effects of stand, climatic and landscape variables on species richness per trap were always consistent between staphylinid-included and staphylinid-excluded assemblages. However, in the case of traps with high staphylinid richness, the effect of the climatic variable, mean temperature of the warmest quarter, was significant on the staphylinid-excluded assemblage, but not on the whole assemblage.

Environmental drivers of variations in species composition

From the CAP results, a uniform and significant response of the intrinsic contributions to inertia of selected variables was observed with both the staphylinid-included and the staphylinid-excluded species assemblages. Deadwood amount was the most powerful explanatory variable (table 3).

(2) Response of staphylinid-restricted assemblages

At the stand level, the Spearman correlation value between species richness in staphylinid-restricted versus staphylinid-excluded assemblages was lower than the staphylinid-included/staphylinid-excluded correlation but remained significant (rho = 0.74; fig. 1d). The Mantel correlation value was low but still significant between staphylinid-restricted and staphylinid-excluded distance matrices ($r = 0.18$, $P < 0.001$; fig. 1e). At the forest site level, species richness values were less correlated in staphylinid-restricted versus staphylinid-excluded assemblages (rho = 0.78; fig. 1f) than in staphylinid-included versus staphylinid-excluded assemblages.

Environmental drivers of variations in species richness

The effects of stand, climatic and landscape variables on species richness per trap were not always consistent between staphylinid-restricted and staphylinid-excluded assemblages (table 2). Deadwood amount and mean temperature of the warmest quarter had a significant effect on species richness per trap in the staphylinid-excluded data, whereas they did not significantly affect the species richness per trap in the staphylinid-restricted data.

Environmental drivers of assemblage variations

In comparison with staphylinid-excluded assemblages, staphylinid-restricted assemblages were far less influenced by selected environmental variables: five out of nine predictors did not have a significant intrinsic contribution to inertia (table 3). Unlike staphylinid-excluded assemblages, staphylinid-restricted assemblages were not significantly influenced by management treatment by a surrounding landscape cover of conifer-dominated forests or by bio-climatic variables (table 3). Like staphylinid-excluded assemblages, staphylinid-restricted assemblages were affected by a surrounding landscape cover of deciduous-dominated forests, by local

Table 3. CAP used to partition the variation in the response species-plot matrix with respect to the combination of explanatory variables (macro-climate, stand and landscape). Only the intrinsic contribution to inertia of each variable is displayed.

	Staphylinid-included			Staphylinid-excluded			Staphylinid-restricted		
	Var	%	Signif.	Var	%	Signif.	Var	%	Signif.
Deadwood amount	1.69	0.44	**	1.7	0.43	**	1.61	0.49	**
Protection	1.14	0.29	**	1.19	0.3	**	0.34	0.1	ns
Elevation	0.9	0.23	**	0.91	0.23	**	0.43	0.13	*
Veteran trees	0.94	0.24	**	0.93	0.24	**	0.65	0.2	**
bio_10	0.71	0.18	**	0.71	0.18	**	0.41	0.12	ns
bio_18	0.81	0.21	**	0.82	0.21	**	0.38	0.12	ns
Deciduous3000 m	0.89	0.23	**	0.89	0.23	**	0.67	0.2	**
Conifer3000 m	0.58	0.15	**	0.6	0.15	**	0.29	0.09	ns
Urban3000 m	0.58	0.15	**	0.57	0.15	**	0.32	0.1	ns

Signif. codes: ***$P<0.001$, ** $0.01>P>0.001$, * $0.05>P>0.01$, ns $P>0.05$

deadwood amount and by local occurrence of veteran trees. As for staphylinid-excluded assemblages, deadwood amount had the most important intrinsic contribution to inertia.

Mean temperature and deadwood amount did significantly affect the species richness of staphylinid-excluded assemblages, but not of staphylinid-restricted assemblages.

Discussion

To include or exclude staphylinids?

In beech-dominated forests, the contribution of rove beetles to the species richness of saproxylic beetle assemblages was important on average, and particularly so in managed stands, in deciduous-dominated landscapes, in deadwood-poor forests and in lowlands. This shows the important role rove beetles should play in biodiversity monitoring in managed forests at low altitudes; however, these types of forests are not currently the focus of much recent research (e.g., Carnus *et al.*, 2006). These findings clearly support the interest of our study on the impact on ecological results of taking into account this species-rich family or not.

From our evaluation of the effects of Staphylinidae family exclusion on results in ecological studies, we can infer that simplified staphylinid-excluded assemblages are relevant surrogates for whole assemblages. The species richness and composition of assemblages with or without staphylinids consistently co-varied. At the stand and forest site levels, the species richness values of the total assemblage and the staphylinid-excluded assemblage were highly positively correlated. Ranking procedures, with and without Staphylinidae included in species richness, gave consistent and similar results at both local and regional scales. The congruency of stand ranking using the whole or the staphylinid-excluded data for species richness calculations was the same in unmanaged and in managed stands. Moreover, the distance matrices based on both types of assemblages also strongly correlated. Indeed, species richness and composition of saproxylic beetle assemblages, with or without staphylinids, congruently responded to landscape, climatic and stand gradients. The staphylinid-included and the staphylinid-excluded assemblages were generally influenced by similar environmental drivers (deadwood amount, temperature, and elevation), with a greater part of variance explained for staphylinid-excluded assemblages. Therefore, the difference in R^2 between models based on staphylinid-included or excluded datasets was low, and we cannot draw conclusions on this point.

Overall, excluding Staphylinidae from saproxylic beetle assemblages did not lead to irrelevant estimations at local or regional scales, contrary to analyses based on data from poorly replicated designs (Parmain *et al.*, 2013). Olivier & Beattie (1996) obtained similar identical rankings between sites with a simplified morphospecies approach compared with a detailed species inventory.

Staphylinids as a target group?

Since rove beetle species are numerous, easily caught in window-flight traps in various forest conditions, the Staphylinidae family could legitimately be suggested as a potential surrogate group reflecting saproxylic beetles as a whole. Indeed, they are often used in other types of monitoring (e.g., pitfall traps; Buse & Good, 1993). Nevertheless, according to our results in European beech forests, the response of staphylinid-restricted assemblages to rough ecological gradients did not reflect the response of other saproxylic beetle families, though at the stand and the forest site levels, their species richness was significantly correlated. While investigating the surrogate power of four other single saproxylic beetle families, Sebek *et al.* (2012) observed the highest correlation between within-family and total richness for Cerambycidae (rho = 0.50). In our study, we found higher correlation values for Staphylinidae (rho = 0.68). However, the environmental drivers of species richness and composition of staphylinid-excluded or staphylinid-restricted assemblages differed. Moreover, the distance matrices based on the two types of assemblages converged only slightly.

Even though Bohac (1999) proposed the use of rove beetle assemblages as bio-indicators for human land use in semi-natural and urban areas, we do not recommend their use as indicators of saproxylic assemblages in a forest context.

Perspectives

We studied saproxylic beetle assemblages only in terms of species richness and composition. Further approaches could focus on the guild structure and the conservation interest of the community. Such research would need to confront the lack of knowledge on rove beetle biology and rarity status. Furthermore, the data that do exist indicate that staphylinid species that have been recorded as predators specialists are

probably more opportunistic than was predicted (e.g., Horák *et al.*, 2011). Furthermore, as alluded to in the introduction, many staphylinid species have undescribed larvae and the females of several species are not distinguishable from other species (e.g., *Scaphisoma* sp.). Staphylinidae are known to have large ecological niches (Bohac, 1999); most of them live in highly variable environments as generalist predators in soil litter or as parasitoids of Dipteran pupae (i.e., Aleocharinae). Their detailed ecological requirements and association to deadwood microhabitats, as well as their rarity status and distribution patterns remain poorly known for many species. Falsely identified saproxylic staphylinid species may therefore weaken, disturb or, in the worst case, invert the relationships pattern between species and environmental conditions. Further ecological and taxonomical research on Staphylinidae is thus urgently needed.

The saproxylic beetle group is family-rich, with more than 70 families in France alone (Bouget *et al.*, 2008). Beetle families other than Staphylinidae may also be time-consuming to identify, and are sometimes excluded from assemblage analyses. These neglected families may concern key feeding groups of specialized species, such as Ciidae, a fungus-eating species, or they may include threatened and often regionally red-listed species such as Aderidae. Their exclusion may lead to biases in the identification of conservation sites and in functional community analyses. The costs and benefits of family exclusion versus exhaustiveness in beetle biodiversity assessment – especially rapid biodiversity assessments (Sebek et al., 2012) – should be further investigated. Finally, our study was based only on European beech forests, and it would be informative to conduct similar analyses in differing forest settings, for instance in European temperate oak forests or in conifer-dominated boreal forests.

The supplementary material for this article can be found at http://www.journals.cambridge.org/BER

ACKNOWLEDGEMENTS

We are grateful to Y. Paillet, B. Nusillard, C. Moliard (Irstea), T. Noblecourt, T. Barnouin, F. Soldati (ONF), F. Köhler, U. Bense, L. Zapponi, H. Bussler, and all the local forest managers for their field and laboratory work, to F. Gosselin (Irstea) for helpful comments on statistical analyses, L. Cizek and J. Schlaghamerský for helpful comments on a previous draft of the paper, and to Vicki Moore who checked the English language. We are undebtfull to two anonymous reviewers for their helpful comments. Data collection in Italy was supported by the LIFE project ManFor C.BD. (LIFE09 ENV/IT/000078). This study was partly supported by CIGA ČZU 20144302 'Managed forests in lowlands and their potential from the perspective of two distinct taxa – beetles and birds'.

References

Alinvi, O., Ball, J., Danell, K., Hjältén, J. & Pettersson, R. (2007) Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. *Journal of Insect Conservation* **11**, 99–112.

Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* **84**, 511–525.

Assing, V. & Schülke, M. (eds) (2011) *Die Käfer Mitteleuropas. Band 4. Staphylinidae I. Zweite Neubearbeitete Auflage*. Heidelberg, Spektrum Akademischer Verlag, I-XII, pp. 1–560.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) *Lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.0–6. Available online at http://CRAN.R-project.org/package=lme4

Beattie, A.J. & Olivier, I. (1994) Taxonomic minimalism. *Trends in Ecology and Evolution* **9**, 488–490.

Bohac, J. (1999) Staphylinid beetles as bioindicators. *Agriculture, Ecosystems and Environment* **74**, 357–372.

Bouget, C., Brustel, H. & Zagatti, P. (2008) The French Information System on Saproxylic BEetle Ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation status. *Revue Ecologie (Terre et Vie)* **63**, 25–28.

Bouget, C., Larrieu, L. & Brin, A. (2014) Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators* **36**, 656–664.

Brunke, A., Klimaszewski, J. & Anderson, R.S. (2012) Present taxonomic work on Staphylinidae (Coleoptera) in Canada: progress against all odds. *ZooKeys* **186**, 1–5.

Buse, A. & Good, J.E.G. (1993) The effects of conifer forest design and management on abundance and diversity of rove beetles (Coleoptera: Staphylinidae): implications for conservation. *Biological Conservation* **64**, 67–76.

Carnus, J.M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A. & Walters, B. (2006) Planted forests and biodiversity. *Journal of Forestry* **104**, 65–77.

Davies, Z.G., Tyler, C., Stewart, G.B. & Pullin, A.S. (2008) Are current management recommendations for saproxylic invertebrates effective? A systematic review. *Biodiversity and Conservation* **17**, 209–234.

Derraik, J.G.B., Closs, G.P., Dickinson, K.J.M., Sirvid, P., Barratt, B.I.P. & Patrick, B.H. (2002) Arthropod morphospecies versus taxonomic species: a case study with araneae, coleoptera, and lepidoptera. *Conservation Biology* **16**, 1015–1023.

Gossner, M.M., Lachat, T., Brunet, J., Isacsoon, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W. & Müller, J. (2013) Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conservation Biology* **27**, 605–614.

Grove, S.J. (2002) The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biological Conservation* **104**, 149–171.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.

Horák, J., Chobot, K., Gabriš, R., Jelínek, J., Konvička, O., Krejčík, S. & Sabol, O. (2011) Uphill distributional shift of endangered habitat specialist. *Journal of Insect Conservation* **15**, 743–746.

Kennedy, A.D. & Jacoby, C.A. (1997) Biological indicators of marine environmental health: Meiofauna – A neglected benthic component? *Environmental Monitoring and Assessment* **54**, 47–68.

Kim, K.C. & Byrne, L.B. (2006) Biodiversity loss and the taxonomic bottleneck: emerging biodiversity science. *Ecological Researches* **21**, 794–810.

Köhler, F. (2010) *Die klimabedingte Veränderung der Totholzkäferfauna (Coleoptera) des nördlichen Rheinlandes – Analysen zur Gesamtfauna und am Beispiel von Wiederholungsuntersuchungen in ausgewählten Naturwaldzellen*. Arnberg, Germany, Landesbetrieb Wald und Holz NRW.

Lachat, T., Wermelinger, B., Gossner, M.M., Bussler, H., Isacsson, G. & Müller, J. (2012) Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecological Indicators* **23**, 323–331.

Langor, D.W., Spence, J.R., Hammond, H.E., James, J.J. & Cobb, T.P. (2006) Maintaining Saproxylic insects in Canada's extensively managed boreal forests: a review. pp. 109 *in* Grove, S.J. & Hanula, J.L. (*Eds*), *Insect Biodiversity and Dead Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology*. Gen. Tech. Rep. SRS–93. Asheville, NC, U.S. Department of Agriculture, Forest Service, Southern Research Station.

Löbl, I. & Smetana, A. (2004) *Catalog of the Palaearctic Coleoptera, Volume 2 – Hydrophiloidea, Histeroidea, Staphylinoidea*, pp. 942 Stenstrup, Apollo Books.

Lohse, G.A. (1964) Staphylinidae I. (Micropeplinae bis Tachyporinae). pp 364 *in* Freude, H., Harde, W., Lohse, G.A. (*Eds*), *Die Kafer Mitteleuropas*. Krefeld, Goecke and Evers.

Lohse, G.A., Benick, G. & Likovsky, Z. (1974) Staphylinidae II. (Hypocyphtinae bis Aleocharinae). pp. 304 *in* Freude, H., Harde, W. & Lohse, G.A. (*Eds*), *Die Kafer Mitteleuropas*. Krefeld, Goecke and Evers.

Müller, J. & Brandl, R. (2009) Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *Journal of Applied Ecology* **46**, 897–905.

Müller, J. & Gossner, M. (2010) Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. *Biological Conservation* **143**, 625–633.

Müller, J., Brunet, J., Brin, A., Bouget, C., Brustel, H., Bussler, H., Förster, B., Isacsson, G., Köhler, F., Lachat, T. & Gossner, M.M. (2013) Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. *Insect Conservation and Diversity* **6**, 162–169.

Müller, J., Bussler, H. & Kneib, T. (2008) Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *Journal of Insect Conservation* **12**, 107–124.

Nieto, A. & Alexander, K.N.A. (2010) *European Red List of Saproxylic Beetles*, p. 56. Luxembourg, Publications Office of the European Union.

Obrist, M.K. & Duelli, P. (2010) Rapid biodiversity assessment of arthropods for monitoring average local species richness and related ecosystem services. *Biodiversity and Conservation* **19**, 2201–2220.

Ohsawa, M. (2007) The role of isolated old oak trees in maintaining beetle diversity within larch plantations in the central mountainous region of Japan. *Forest Ecology and Management* **250**, 215–226.

Olivier, I. & Beattie, A.J. (1996) Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* **10**, 99–109.

Parmain, G., Dufrêne, M., Brin, A. & Bouget, C. (2013) Influence of sampling effort on saproxylic beetle diversity assessment: implications for insect monitoring studies in European temperate forests. *Agricultural and Forest Entomology* **15**, 135–145.

R Core Team. (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available online at URL http://www.R-project.org/.

Schmidl, J. & Bussler, H. (2004) Ökologische Gilden xylobionter Käfer Deutschlands und ihr Einsatz in der landschaftsökologischen Praxis – ein Bearbeitungsstandard. *Naturschutz und Landschaftsplanung* **36**, 202–218.

Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F., Meriguet, B., Micas, L., Noblecourt, T., Rose, O., Velle, L. & Bouget, C. (2012) A test for assessment of saproxylic beetle biodiversity using subsets of "monitoring species". *Ecological Indicators* **20**, 304–315.

Siitonen, J. (2001) Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. *Ecological Bulletins* **49**, 11–41.

Siitonen, J. & Saaristo, L. (2000) Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological conservation* **94**, 211–220.

Stokland, J.N. & Meyke, E. (2008) The Nordic saproxylic database: an emerging overview of the biological diversity in dead wood. *Revue d'Écologie (Terre Vie)* **63**, 29–40.

Stokland, J., Tomter, S. & Söderberg, U. (2004) Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. pp. 207–226 *in* Marchetti, M. (*Ed.*) *Monitoring and Indicators of Forest Biodiversity in Europe – From Ideas to Operationality*, Vol. 51. EFI workshop, November 12th–15th 2003, Firenze, Italy.

Terlizzi, A., Bevilacqua, S., Fraschetti, S. & Boreo, F. (2003) Taxonomic sufficiency and the increasing insufficiency of taxonomic expertise. *Marine Pollution Bulletin* **46**, 556–561.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Svedrup-Thygeson, A. & Mönkkönen, M. (2010) Woodland key habitats in northern Europe: concepts, inventory and protection. *Scandinavian Journal of Forest Research* **25**, 309–324.

Williams, P.H. & Gaston, K.J. (1994) Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation* **67**, 211–217.

Article 5: Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles?

Animal Conservation. Print ISSN 1367-9430

Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles?

C. Bouget[1], G. Parmain[1,2,3], O. Gilg[4], T. Noblecourt[2], B. Nusillard[1], Y. Paillet[1], C. Pernot[1], L. Larrieu[5,6] & F. Gosselin[1]

1 'Forest ecosystems' Research Unit, National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), Nogent-sur-Vernisson, France
2 National Laboratory of Forest Entomology, National Forest Office (ONF), Quillan, France
3 Natural Patrimony Department, National Museum of Natural History, Paris, France
4 Réserves Naturelles de France, Quétigny, France
5 UMR 1201 Dynafor, INRA, INPT/ENSAT/EIPURPAN, Castanet-Tolosan, France
6 CNPF-IDF, Auzeville Tolosane, France

Keywords
delayed harvesting; forest reserves; temperate deciduous forests; insect biodiversity; deadwood; tree microhabitats.

Correspondence
Christophe Bouget, EFNO, Irstea, Domaine des Barres, Nogent-sur-Vernisson 45290, France. Email: christophe.bouget@irstea.fr

Editor: Darren Evans
Associate Editor: Nick Isaac

Received 06 May 2013; accepted 28 November 2013

doi:10.1111/acv.12101

Abstract

The decline of many saproxylic species results from the decrease in old-growth structures in European harvested forests. Among conservation tools, protected reserves withdrawn from regular harvesting and extended rotations have been employed to restore old-growth attributes in structurally simplified managed forests, even if the effects of such management actions on forest habitats and biodiversity remain largely unknown.

In this study, we compared structural stand features and saproxylic beetle assemblages in two stand classes – recently harvested stands and long-established reserves, where less or more than 30 years had elapsed since last harvest. Habitat and saproxylic beetle data were collected according to standardized protocols in 153 plots in seven lowland deciduous forests.

Tangible contrasts in stand features were found between long-established reserves and recently harvested plots. Indeed, most higher-value densities and volumes were found in unharvested areas. The difference was weaker for microhabitat-bearing tree density than for deadwood; some deadwood features, such as volume of large downed and standing deadwood showed a very pronounced difference, thus indicating a marked deleterious effect of forest harvesting on these elements. Deadwood diversity, on the other hand, was only slightly affected and the level of stand openness did not change.

The response of saproxylic beetles to delayed harvesting was weaker than the structural changes in deadwood features. Nevertheless, long-established reserves showed higher species richness and slightly but significantly dissimilar species assemblages than recently harvested plots. Indeed even if only some guilds weakly increased in non-harvested plots, harvesting classes significantly affected the abundance of a quarter of the species tested.

Our results tend to question measures such as rotating and temporarily ageing patches. We argue in favor of permanent strict fixed-location reserves. Future work should examine how stands recover old-growth forest attributes and how the associated saproxylic fauna colonizes in the long term.

Introduction

European forest dynamics has been deeply affected by forestry and forest fragmentation for millennia (Peterken, 1996). Stand composition and structure have been greatly simplified by harvesting and other uses, even in remote areas. Several studies demonstrated the negative effects of conventional management practices on old-growth structures (e.g. Burrascano *et al.*, 2013; Green & Peterken, 1997; Lombardi *et al.*, 2008). Structural simplification has been shown to result in the decline of many associated saproxylic populations, but the issue has received more attention in

North America and northern Europe than in central and southern Europe (e.g. Martikainen *et al.*, 2000; Grove, 2002).

In forests subjected to structural simplification through harvesting, strategies to restore old-growth attributes may involve (1) setting aside forest plots, (2) extended rotations, (3) retention of structural features at the time of harvest and (Keeton, 2006) (4) man-made restoration of structural elements (Martikainen *et al.*, 2000). In the last 20 years, there has been an increasing focus on systematic conservation planning, that is how to select protected areas in a way that captures biodiversity as efficiently as possible (e.g. Margules & Pressey, 2000). Protected forests include different protection categories and surface areas (Schmitt *et al.*, 2009) and they are described worldwide in countless ways. Areas 'left for natural dynamics' can be found in several protection categories often as (so-called) strict forest reserves, where neither silvicultural intervention nor any other avoidable human impacts are allowed, but other denominations abound: wilderness areas, areas withdrawn from regular management, abandoned, unharvested, set-aside forest areas or unmanaged core areas in national parks. Among passive restoration strategies (Bauhus, Puettmann & Messier, 2009), small-scale management tools such as delaying harvesting, leaving unharvested patches or preserving habitat trees (Lachat & Bütler, 2009) have been employed to increase the number of old-growth structures in forests (Bauhus *et al.*, 2009). Other examples include woodland-key habitats, green-tree retention patches left in clearcuts as short-term refuges or lifeboats for many organisms during the regeneration phase in Scandinavia and North America (e.g. Vanha-Majamaa & Jalonen, 2001, Aubry *et al.*, 1999), ageing or old-growth patches kept as portions of management units in France (Lassauce *et al.*, 2013). Despite an increase in the number of empirical studies concerning the effects of forest abandonment on species diversity (see Paillet *et al.*, 2010), the relative efficiency of each management strategy in supporting biodiversity remains unknown. When harvesting activities are delayed for several decades, natural forest dynamics may bring about structural changes that restore old-growth attributes, depending on site potential (Vandekerkhove *et al.*, 2009): larger trees, heterogeneous vertical and horizontal structure with greater variations in tree size, age, spacing and species composition, increased supplies of deadwood, more large snags and fallen trees, multiple canopy layers, changes in disturbance regime, canopy gaps and understory patchiness. These structural changes have been recorded in several case studies (e.g. Lassauce *et al.*, 2012, 2013, Sitzia *et al.*, 2012) and may impact biodiversity.

In this study, we compared the habitat parameters and the diversity of saproxylic beetles (i.e. abundance, species richness and composition) in set-aside and harvested areas in seven lowland deciduous French forests. The issues were addressed in two steps: (1) How were saproxylic habitat parameters, such as the diversity and density of deadwood and tree microhabitats, affected in long-established set-aside plots compared with recently harvested plots? (2) Did saproxylic beetle assemblages (including rare species) respond to these habitat changes?

Material and methods

Study areas

The plots were located in seven lowland beech, *Fagus sylvatica* L., and oak, *Quercus robur* L and *Q. petraea* (Mattus.) Liebl., forests (Table 1) in the Atlantic or Continental biogeographic domain. Each forest was several hundred kilometers from the others: one in western France (Chize), three in eastern France (Auberive, Citeaux, Combe-Lavaux), one in central France (Troncais) and two in northern France (Rambouillet, Fontainebleau). The plots in each forest were several hundred meters apart. A design of 153 plots was set up in managed stands (98) and in recently (16) or long-established (39) forest reserves. Managed forests were coppice-with-standards under conversion to high forest (33), even-aged (54) or uneven-aged (11) high forests (see Supporting Information Table S1). All plots were located in mature stands before regeneration felling or final cut. Last harvests consist of thinning operations in even-aged high forests and single tree removals in coppice-with-standards stands under conversion and uneven-aged high forests. The time elapsed from last harvest was postulated

Table 1 Sampling design layout. Among long-established reserves (L-UNH), old (> 30 years) and very old reserves (> 100 years) were not tested separately due to the small number of replicates available in the latter category. Managed plots and recently established reserves are grouped in R-HAR. Sampling year between brackets

	Beech			Oak			
		L-UNH > 30 yrs			L-UNH > 30 yrs		
	R-HAR < 30 years	30–100 years	> 100 years	R-HAR < 30 years	30–100 years	> 100 years	Total
Auberive [2009]	11	4		7	2		24
Chize [2010]	10	2		12			24
Citeaux [2010]				6	6		12
Combe-Lavaux [2010]	3	2		1	2		8
Fontainebleau [2008]	5	3	9	7			24
Rambouillet [2007]				24	6		30
Troncais [2009]				28	3		31
Total	29	11	9	85	19	0	153

for each plot based on management plans, reports or information from local managers. Unlike Christensen *et al.* (2005), we did not derive the number of years since last harvest from the official establishment date of the reserves as these do not necessarily coincide. Because the time since last harvest was not precisely known in several cases, we classified the plots into two harvesting classes based on the best estimate of the length of time without harvesting or removal of trees and deadwood (Table 1): 'recently harvested' (R-HAR < 30 years ago, $n = 114$), including harvested plots ($n = 98$) and recently established reserves ($n = 16$); or long-established reserves (L-UNH > 30 years, $n = 39$), including old (> 30 years and < 100 years, $n = 30$) and very old reserves (> 100 years, $n = 9$). Very old reserves were found in the Fontainebleau state forest only. We collected environmental and entomological data following standardized protocols.

Beetle sampling and identification, species characterization

Flying saproxylic beetles were sampled by two cross-vane flight interception traps (Polytrap™, E.I. Purpan, Toulouse, France) per plot, set about 20 m from each other, for a total number of 306 traps. The unbaited traps were suspended roughly 1.5 m above ground. Active insects were collected from April to August during 1 year. For each species in all the taxa from the ±50 families recorded, we characterized degree of geographic rarity in France according to the FRISBEE database (http://frisbee.nogent.cemagref.fr/index.php/en/) and distinguished common (abundant and/or widely distributed) and rare (not abundant and only locally distributed) species. All species were assigned to one saproxylic trophic group, but only the four main guilds were studied (xylomycetophagous, xylophagous, saproxylophagous and zoophagous).

Stand and deadwood variables

We used a combination of fixed-area and fixed-angle techniques to estimate (1) wood volumes for live trees, snags, logs and stumps, and (2) the basal area of live trees on 0.15 ha (Fontainebleau, Auberive, Chize, Citeaux, Combe-Lavaux) or 0.30 ha (Rambouillet, Troncais) plots. We set a minimum diameter of 7.5 cm for live trees, snags and logs.

Four variables were used to describe the deadwood: tree species, diameter (six classes: 5, 10–15, 20–25, 30–40, 50–65, > 70 cm), position (log, snag, stump), decay stage [nine classes adapted from Sippola, Siitonen & Kallio (1998) and Larjavaara & Muller-Landau (2010) and crossing three classes of remaining bark cover (from 95% of the stem still covered by attached bark to missing bark over the whole stem) and three classes of inner wood hardness assessed by 'knife penetration test' (from hard outer wood to deeply disintegrated and soft inner wood)]. A deadwood diversity index was calculated as the number of observed deadwood types, that is the number of combinations of the above four variables (tree species × diameter class × decay class × position), as suggested by Siitonen *et al.* (2000). The volume of live trees was calculated using wood volume tables based on the dbh variable, and used to estimate the deadwood volume ratio (= dead wood/(live + dead wood)), accounting for site productivity (Hahn & Christensen, 2004). Based on the deadwood surveys, we selected seven deadwood variables for analysis: (1) deadwood volume, (2) deadwood volume ratio, (3) number of deadwood types, (4) standing deadwood volume, (5) large standing deadwood (diameter > 40 cm) volume, (6) downed deadwood volume, and (7) large downed deadwood (diameter > 40 cm) volume. The thresholds defining large deadwood, large and very large trees were inspired by results in Nilsson *et al.* (2003) and Larrieu & Cabanettes (2012).

The basal area of large trees (67.5 < dbh ≤ 87.5 cm) and very large trees (dbh > 87.5 cm) were measured on 0.15–0.3 ha plots; the density of large trees was also inventoried in 1-ha circular plots. Tree microhabitat densities were inventoried during leaf-burst in 1-ha circular plots centered around the two flight traps. We recorded seven microhabitat types borne by live trees (Larrieu & Cabanettes, 2012): (1) 'empty' cavities, (2) cavities with mould, (3) fruiting bodies of saproxylic fungi, (4) sap runs, (5) dead branches, (6) tree crown deadwood, and (7) missing bark [i.e. hard patches of wood with no bark > 600 cm^2] (see Table 2 for further details on predictors). Microhabitats other than crown deadwood were only recorded when visible on the trunk beneath and within the tree crown. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type. The total density of microhabitats, the number of microhabitat types (among the seven observed types) and the individual densities of four microhabitat types ('empty' and mould cavities pooled, dead branches and tree crown deadwood pooled, sporocarps of saproxylic fungi and sap runs) were considered for analysis. Stand openness was assessed as the total proportion of open areas (clearings, edges, stand surface with a well-developed herb layer composed of flowering plants) in a 1 ha plot. For further details on how the environmental variables were measured, see Bouget *et al.* (2013).

Data analysis

Our main objectives were to compare (1) stand structural characteristics and (2) saproxylic beetle assemblages in the two stand classes (R-HAR and L-UNH) based on the amount of time elapsed since last harvest. Because the same set of environmental variables was used for both traps in the same plot, the catches of the two traps were combined prior to analyses carried out at the plot level.

The differences in mean values of structural stand features between recently harvested and long-established reserves were analyzed with a Generalized Gaussian or Poisson Linear Mixed Model where 'forest' was a spatially implicit random effect on the intercept (lmer function in lme4 R-package).

Table 2 Effect of the harvesting class on stand characteristics (deadwood, microhabitat, large trees, openness)

	Factor	Detail	Signif	Est R-HAR	Est L-UNH	Ratio	Error distribution family
Stand features	Basal area of large trees	Basal area of large trees in a 0.3 ha plot (67.5 < dbh ≤ 87.5 cm) (m^2 ha^{-1})	***	2.957 (1.579)	7.198 (1.663)	2.43	Gaussian
	Basal area of very large trees	Basal area of the very large trees in a 0.3 ha plot (dbh > 87.5 cm) (m^2 ha^{-1})	***	0.501 (0.591)	2.405 (0.628)	4.80	Gaussian
	Density of large trees	Number of large trees in a 1 ha plot (dbh > 67. 5 cm)	***	1.389 (0.487)	2.116 (0.487)	1.52	Poisson
	Openness	Proportion in cumulative area of open areas (clearings, edges, areas with a well-developed herb layer composed of flowering plants) (%) in a circular 1 ha plot	NS	12.490 (5.188)	11.667 (5.962)		Gaussian
MH features	Density of microhabitat-bearing trees	Total density of microhabitat-bearing trees in a 1 ha plot	***	2.647 (0.129)	3.046 (0.131)	1.15	Poisson
	Number of microhabitat types	Number of microhabitat types in a 1 ha plot	**	1.468 (0.061)	1.702 (0.070)	1.16	Poisson
	Density of cavity-bearing trees	Density of cavity-bearing trees in a 1 ha plot: 'empty' cavities with an entrance above 3 cm in width, woodpecker breeding and feeding holes, deep cavities formed between roots, cavities with mould with an entrance above 10 cm in width	***	1.620 (0.093)	2.208 (0.098)	1.36	Poisson
	Density of fungus-bearing trees	Density of fungus-bearing trees in a 1 ha plot: fruiting bodies of tough or pulpy saproxylic fungi, > 5 cm in diameter	***	0.397 (0.203)	0.458 (0.208)	1.15	Poisson
	Density of deadwood-bearing trees	Density of deadwood-bearing trees a 1 ha plot: crown deadwood in (large dead branches > 20 cm in diameter and > 1 m in length, crown deadwood volume > 20% of the total crown wood volume)	**	1.624 (0.276)	1.824 (0.278)	1.12	Poisson
	Density of sap-run-bearing trees	Density of sap-run-bearing trees: sap runs > 10 cm in length in a 1 ha plot	NS	−1.142 (0.327)	−1.359 (0.394)		Poisson
DW features	Deadwood volume	Total volume of deadwood in a 0.3 ha plot (m^3 ha^{-1})	***	22.677 (9.539)	79.976 (10.992)	3.53	Gaussian
	Deadwood ratio	Volume ratio = deadwood /(Live trees+deadwood)	***	0.099 (0.025)	0.225 (0.030)	2.27	Gaussian
	Large downed deadwood volume	Volume of large downed deadwood (> 40 cm in diameter) in a 0.3 ha plot (m^3 ha^{-1})	***	3.052 (4.029)	27.387 (4.875)	8.97	Gaussian
	Large standing deadwood volume	Volume of large standing deadwood (> 40 cm in diameter)) in a 0.3 ha plot (m^3 ha^{-1})	***	2.123 (3.067)	18.658 (3.701)	8.79	Gaussian
	Standing deadwood volume	Volume of standing deadwood (> 10 cm in diameter) in a 0.3 ha plot (m^3 ha^{-1})	***	4.529 (2.811)	21.910 (3.572)	4.84	Gaussian
	Downed deadwood volume	Volume of downed deadwood (> 10 cm in diameter) in a 0.3 ha plot (m^3 ha^{-1})	***	16.791 (7.487)	57.373 (8.684)	3.42	Gaussian
	Number of deadwood types	Nb deadwood types (tree species*diameter*decay*position)	**	2.400 (0.243)	2.559 (0.245)	1.07	Poisson

Stands were classified as recently managed (R-HAR < 30 years ago) or long-established reserves (L-UNH > 30 years ago). Differences in stand features between the two harvesting classes were tested with a linear mixed model (NS = not significant; *0.05 > P > 0.01; **0.05 > P > 0.001; ***P < 0.001). Ratio = ratio dividing estimates of L-UNH by R-HAR (see Material and Methods) (SE between parentheses).

To rank the effect of the harvesting variable among structural predictors of variations in common or rare species richness, we assessed the multimodel-averaged estimates (Burnham & Anderson, 2002) determining the response of species richness to stand features. As colinearity among predictor variables may lead to unreliable parameter estimates, we implemented the strategy suggested by Zuur, Ieno & Elphick (2010) to address multicolinearity before model averaging. We sequentially dropped the covariate with the highest variance inflation factor (VIF), then recalculated the VIFs and repeated this process until all VIFs were below a preselected threshold (Zuur *et al.*, 2010 suggest a cut off at 3). We used the 'vif.mer' function to calculate VIFs for linear mixed-effects models built using the lmer function in the 'lme4' package (Table 2). As the relationship between species richness and deadwood volumes is better described by semi-log models (Martikainen *et al.*, 2000), we used (log x+1)-transformed values for deadwood volumes. The selected variables with VIF < 3 were: harvesting class, openness, basal area of very large trees (dbh > 87.5 cm), large tree 1 ha density, density of sap-run-bearing trees, density of fungus-bearing trees, density of cavity-bearing trees, density of crown deadwood-bearing trees, number of microhabitat types, total deadwood volume, deadwood ratio, log10 (large downed deadwood volume), log10 (large standing deadwood volume). For each response variable, we generated the null model and generalized linear mixed models (Poisson error structure) with all the combinations of two explanatory variables. Using the differences in the Akaike information criterion (AICc) scores between each model and the best model (ΔAICc) as well as the Akaike weights for each model, we calculated the model-averaged estimates. Only significant variables ($P < 0.10$ across all the models) were displayed (lme4, MuMIn, arm; R-packages).

To rank the effect of the harvesting variable among structural predictors on variations in species composition (including singletons), we performed a Canonical Analysis of Principal coordinates (vegan R-package, CAP, Anderson & Willis, 2003). Based on Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, as colinearity among predictor variables is not considered to be a problem in CAP. We calculated total constrained inertia, the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance (permutation tests – 100 runs) and the relative contribution of each set of variables (deadwood, microhabitat, stand, forest, harvesting class) to constrained inertia. In addition, we used a pairwise ANOSIM procedure based on Jaccard distance matrices to test for differences in assemblage composition among predefined groups with spatially constrained permutation tests (Clarke, 1993); the grouping factor was the harvesting treatment and the spatial constraint the forest.

We also used a generalized linear mixed model, with a spatially implicit variable (forest) as a random factor on the intercept and a Poisson error distribution, to analyze the differences between the two harvesting classes in (1) mean abundance and richness per plot of rare or common species and trophic groups, and (2) mean abundance of selected species (more than 20 individuals caught and occurring in at least 10 out of the 153 plots in our data set). Since we found a close correlation between total abundance and the number of beetle species recorded on a plot, we used the number of individuals as a covariate in the richness models (Gotelli & Colwell, 2001) to separate the effects on the number of individuals from species effects. To analyze differences in occurrence per plot of selected beetle species between the two harvesting classes, we used a generalized linear mixed model with a binomial error structure and 'forest' as a spatial random effect (lmer function in lme4 R-package). In order to quantify the magnitude of significant differences between R-HAR and L-UNH treatments, we computed an index by dividing model estimates for each of the harvesting treatments (estimate L-UNH/ estimate R-HAR) with 'forest' as a random factor.

All analyses were conducted using R v2.12.0. All R-packages used are available online at http://cran.r-project.org/web/packages/available_packages_by_name.html. The 'vif.mer' function is available online at https://github.com/aufrank/R-hacks/blob/master/mer-utils.R.

Results

Overall, the compiled dataset included 99 383 individuals in 476 beetle species (25 taxa identified at the genus level only), among which 377 common, 69 rare (15% of the total number) and 30 species with an undefined rarity status were recorded.

Habitat parameters in R-HAR plots versus L-UNH

Significant differences in stand features (deadwood, microhabitat, large trees, openness) were measured between L-UNH and R-HAR (Table 2). Values for deadwood (deadwood volume, deadwood ratio, number of deadwood types, downed deadwood volume, large standing deadwood volume, standing deadwood volume, large standing deadwood volume), microhabitats (density of microhabitat-bearing trees, number of microhabitat types, density of cavity-bearing trees, density of deadwood-bearing trees, density of fungus-bearing trees) and large tree characteristics (basal area of large trees and very large trees, density of large trees) were always considerably higher in L-UNH than in R-HAR plots. Deadwood diversity was only slightly, although significantly, higher in L-UNH. Only the density of sap-run-bearing trees and openness values remained significantly unaffected by the harvesting class.

The magnitude of the differences between R-HAR and L-UNH plots was even more pronounced with respect to certain deadwood features. These differences were characterized by a high relative increase from R-HAR to L-UNH that is the ratio dividing estimates in L-UNH by R-HAR for four variables: large downed deadwood volume

(estimate ratio = 8.97), large standing deadwood volume (estimate ratio = 8.79), standing deadwood volume (estimate ratio = 4.84) and basal area of very large trees (estimate ratio = 4.80). This indicates a strong negative effect of forest harvesting on those attributes. According to the estimate ratio, the differences measured between L-UNH and R-HAR plots were even more pronounced for large deadwood volumes than for large tree characteristics. Microhabitat features were not as impacted as were deadwood and stand features by the harvesting class (Table 2).

Saproxylic beetle diversity in R-HAR plots versus L-UNH

Species composition

Variations in total inertia of saproxylic beetle assemblages were explained by geographical (35.0%), deadwood (9.0%), microhabitats (8.8%) and stand structural characteristics (7.0%) (Table 3). Only openness, microhabitat diversity, deadwood ratio and deadwood diversity had a significant ($P < 0.05$), although marginal, contribution to variations in species composition. As along with the density of fungus-bearing trees and large standing deadwood volume, the class of time elapsed since harvesting showed a non-significant trend ($P < 0.1$), accounting for only 1.7% of the constrained inertia. A spatially constrained ANOSIM test also showed slightly, but significantly, dissimilar species assemblages between the harvesting classes (1000 permutations, R: 0.168; significance: 0.002).

Species richness

The class of time elapsed since harvesting was not a key variable for saproxylic beetle species richness; it ranked fifth in explanatory value among the 12 structural stand features and was only slightly significant (Table 4). L-UNH, however, showed a higher saproxylic beetle species richness than R-HAR plots (Table 4). The best models for both rare and common species were the number of deadwood types and openness, and the best for common species was deadwood volume ratio.

Table 3 Ranked effect of the harvesting class among structural and spatial predictors on variations in species composition

	Predictors	Cumulated marginal inertia	%CI
Spatial	Forest**	7.348	34.97%
Set-aside	Harvesting class°	0.357	1.699%
Stand	Basal area of large trees, basal area of very large trees, density of large trees, openness**	1.475	7.019%
MH	Total density of microhabitats, number of microhabitat types*, density of cavity-bearing trees, of fungus-bearing trees°, of deadwood-bearing trees, of sap-run-bearing trees	1.863	8.866%
DW	log10 (Total volume deadwood), Deadwood ratio*, log10 (large downed deadwood volume), log10 (large standing deadwood volume)°, log10 (downed deadwood volume), log10 (standing deadwood volume), Number of deadwood types*	1.899	9.041%

Canonical Analysis of Principal coordinates (CAP) used to partition the variation in the response species-plot matrix with respect to the combination of explanatory stand features (deadwood, microhabitat, large trees, openness); %CI: relative contribution to constrained inertia. Significance of marginal contribution to inertia: °0.1 > P > 0.05; *0.05 > P > 0.01; **0.01 > P > 0.001.

Table 4 Ranked effect of the harvesting class among structural predictors on variations in species richness. Multimodel averaged estimates for structural stand features (deadwood, microhabitats, large trees, openness) and harvesting class determining the response of saproxylic beetle species richness (rare, common). Relative importance is the weight of evidence for each parameter across all the best models combining several variables (mixed-effect models, with forest as a random effect)

species richness	variable	Variable Model-averaged estimate (significance)	Relative contribution	Best models (DeltaAICc < 3)	
Rare	1. Number of deadwood types	1.48***	0.93	divDW+open	AICc = 596.8
	2. Openness	0.81**	0.65		
Common	1. Openness	10.02***	1.00	open+ratio	AICc = 1166.7
	2. Deadwood ratio	6.53***	0.51	divDW +open	AICc = 1167.0
	3. Number of deadwood types	10.81***	0.45		
	4. Harvesting class	3.92°	0.01		
	5. Density of cavity-bearing trees	3.70°	0.01		
	6. log10 (Volume of large downed deadwood)	3.70°	0.01		

Only significant variables (°0.1 > P > 0.05; *0.05 > P > 0.01; **0.01 > P > 0.001; ***P < 0.001) were selected.

Table 5 Values of the estimates (s.e. between parentheses) from generalized linear mixed effect models with a Poisson error distribution for abundance and richness of ecological groups of saproxylic beetles species in 'recently harvested (R-HAR < 30 years ago) or 'long-established reserves' (L-UNH > 30 years ago)

		Abundance		Species richness	
		Estimate R-HAR	Estimate L-UNH	Estimate R-HAR	Estimate L-UNH
Feeding guilds	Mycophagous	4.066 (0.306)	4.201 (0.306)***	2.25 (0.099)	2.395 (0.106)*
	Saproxylophagous	2.345 (0.340)	2.533 (0.341)***	1.339 (0.172)	1.415 (0.180) NS
	Zoophagous	4.029 (0.154)	4.038 (0.155) NS	2.099 (0.119)	2.233 (0.124)*
	Xylophagous	5.056 (0.457)	4.745 (0.457)***	2.65 (0.077)	2.601 (0.084) NS
Rarity groups	Common	5.773 (0.341)	5.572 (0.341)***	3.682 (0.001)	3.776 (0.001)**
	Rare	2.073 (0.431)	2.27 (0.432)***	0.744 (0.184)	0.919 (0.1985) NS
	Total	5.859 (0.326)	5.672 (0.326)***	3.786 (0.001)	3.889 (0.001)***

Probability (*P*) of a significant difference between mean values is indicated by: NS = not significant. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. We used the abundance of a covariate in species richness models.

Guild composition

The abundance of common and xylophagous species was significantly lower in L-UNH than in R-HAR plots. Zoophagous species abundance was not sensitive to the harvesting class. In contrast, mycophagous, saproxylophagous and rare species were more abundant in L-UNH. The number of mycophagous, zoophagous and common species per plot, after accounting for abundance, was slightly, but significantly, higher in L-UNH. For saproxylophagous, xylophagous and rare species, no significant difference in species richness was observed between harvesting classes (Table 5).

Individual species responses

At the individual species level, about 25% ($n = 39$.) of the tested species had a significant response in abundance to the harvesting class. The same proportion of significantly responding species occurred in both harvesting classes: half of the species were significantly more abundant in R-HAR plots, and half were significantly more abundant in L-UNH. Two rare taxa were included among the species responding positively to L-UNH (none were found in R-HAR plots; Table 6).

Table 6 Difference in abundance per plot of selected species between 'recently harvested' (R-HAR < 30 years ago) or 'long-established reserves' (L-UNH > 30 years ago) plots

Abundance > in R-HAR	Abundance > in L-UNH
Ampedus quercicola	*Anaspis flava*
Anaglyptus mysticus	***Anaspis melanopa***
Anostirus purpureus	*Cis boleti*
Aulonothroscus brevicollis	*Clerus mutillarius*
Cyclorhipidion bodoanus	*Corticeus unicolor*
Ernoporicus fagi	*Cryptarcha undata*
Hemicoelus fulvicornis	*Dasytes plumbeus*
Hylecoetus dermestoides	*Dryocoetes villosus*
Leiopus femoratus	*Hylis olexai*
Litargus connexus	*Mycetochara maura*
Megatoma undata	*Mycetophagus ater*(*)
Phymatodes testaceus	*Oxylaemus cylindricus*
Platycerus caraboides	***Paromalus parallelepipedus***
Stenocorus meridianus	*Ptilinus fuscus*(*)
Taphrorychus bicolor	*Rhagium bifasciatum*
Tetratoma ancora	*Scolytus rugulosus*
Vincenzellus ruficollis	*Thanasimus formicarius*
Xyleborinus saxesenii	*Tritoma bipustulata*
Xyleborus dispar	*Trypodendron signatum*
	Xyleborus dryographus

Only significant differences are shown (*P*-value < 0.001 after a Bonferroni correction for 150 tests). Only species sampled in at least 10 plots and with more than 20 individuals were analyzed, with generalized linear mixed-effect models and a binomial error distribution; 'forest' was a random factor. Bold indicates significant in occurrence, (*) indicates rare species.

Discussion

Changes in stand structure induced by non-harvesting

In L-UNH (i.e. plots set-aside for at least 30 years) originating from managed stands, we measured tangible contrasts in stand characteristics compared with R-HAR plots. Indeed, most of the stand characteristics we studied displayed higher volume and density values in long-established set-asides than in R-HAR areas.

More than 30 years without harvesting allowed the deadwood volumes to increase significantly. Vandekerkhove *et al*. (2005) already showed that deadwood can accumulate quite fast in forest reserves, especially in terms of density. In abandoned beech forests in Germany, Meyer & Schmidt (2011) indicated a rather fast relative increase in deadwood volume: total deadwood doubled in about 9 years (standing deadwood in 7 years). Such figures are probably dependent on dominant tree species, soil fertility and the silvicultural stage of the stand at the time it was set aside. Several other studies found a similarly significant increase in deadwood volume in long-unharvested stands compared with managed ones (Kirby, Webster & Antczak, 1991; Sippola *et al*., 1998; Motta *et al*., 2010; Calamini *et al*., 2011), or at least for coarse woody debris (Boncina, 2000; Marage & Lemperiere, 2005; Sitzia *et al*., 2012). Timonen *et al*. (2011) also

demonstrated that deadwood volumes are higher in woodland key habitats than in managed stands.

However, we showed that deadwood diversity only increased slightly in L-UNH (partly due to the lack of large-diameter logs in late decay stages). Nonetheless, in the data compiled by Timonen *et al.* (2011), deadwood diversity was much higher in woodland key habitats compared with managed stands, probably partly because of an initial selection effect, that is deadwood in the selected plots when they were selected as set-asides or as key habitats.

The difference between L-UNH and recently managed plots may be more pronounced with respect to certain deadwood qualities, as suggested by Siitonen *et al.* (2000). In their Finnish study in spruce forests, large dead coniferous and deciduous trees were respectively 25 and 35 times more abundant on average, in unharvested plots than in R-HAR stands. Accordingly, we found a strong impact of harvesting on large dead wood (downed and standing), with a ninefold increase in large deadwood when harvesting is delayed for at least 30 years. This increase in large deadwood was twice as high as for total deadwood volume. Boncina (2000) and Meyer & Schmidt (2011) also found a rapid accumulation of standing deadwood from unmanaged to managed stands.

Nonetheless, more deadwood was found in longer-established beech reserves (Christensen *et al.*, 2005) and in 60-year-old over-mature French coppices compared with 20-year-old mature coppice (Lassauce *et al.*, 2012). Vandekerkhove *et al.* (2009) argued that full natural restoration of deadwood characteristics (with virgin forests in Central Europe as a reference) may be quite long. Furthermore, Larrieu, Cabanettes & Delarue (2012) showed that a 50-year period of non-intervention was too short to develop complete stand maturity in beech-fir stands, even in highly productivity contexts.

Like Bauhus *et al.* (2009), we were able to detect a list of structural elements (deadwood, microhabitats, large trees) which become significantly more frequent in unharvested stands. We also showed, in accordance with the results simulated by Ball, Lindenmayer & Possingham (1999), that the increase in microhabitat-bearing tree density was weaker than the increase in deadwood density. Reaching high levels of microhabitat density requires time, since the probability of microhabitat occurrence or the number of microhabitat types increases with tree diameter (e.g. Larrieu *et al.*, 2012). In a simulation model, Ranius, Niklasson & Berg (2009) pointed out the importance of tree age for cavity formation on trees (see also empirical data in Gibbons, McElhinny & Lindenmayer, 2010). Furthermore, Fan *et al.* (2003; 2005) showed a higher frequency of cavity trees in 120-year-old forests than in younger stands, and in old-growth than in managed stands (like Bauhus *et al.*, 2009). In our results, a slightly higher density of cavity-bearing trees was measured in L-UNH than in R-HAR plots.

Across our sampling design, L-UNH and R-HAR forests did not differ in terms of stand openness, as the stands were too young to be significantly impacted by canopy gap dynamics. Gap dynamics is known to increase average sun exposure in old-growth forests compared with managed stands (Rugani, Diaci & Hladnik, 2013), and open forest habitats are required by a large number of specialized saproxylic species (Vodka, Konvicka & Cizek, 2009).

Effect of non-harvesting on saproxylic beetle assemblages

In our study, the effect of non-harvesting on biodiversity was slightly significant. The class of time elapsed since harvesting seemed to be important for 25% of the tested species, but was not as important a variable as structural parameters for saproxylic beetle assemblages in our data. Some guilds and groups were positively influenced by non-harvesting (mycophagous abundance and richness, saproxylophagous and rare species abundance), but the relationship was weak and clearly had less impact than deadwood features (see Table 2 and Table 4). Many saproxylic species may simply require a small amount of dead wood that is also available in managed forests. Or structural changes in stand characteristics may occur more quickly than the response of saproxylic organisms. Delayed responses by saproxylic beetle communities may be due to the limited ability, at least for old-growth forest specialists, to colonize favorable substrates (dispersal, habitat detection, etc.) and their density-dependence in the colonization process. Local assemblages may be deeply affected over the long term by historical deadwood supplies (Hanski & Ovaskainen, 2002). Furthermore, population levels must reach minimum thresholds for species to be detected. This interpretation is reflected in our study: the two most typically influential variables for saproxylic beetle richness – deadwood diversity and openness – did not respond strongly to more than 30 years without harvesting. Yet, deadwood diversity has been recognized as a key factor for saproxylic beetle diversity in temperate deciduous forests (Bouget *et al.*, 2013) and other studies based on similar time frames have demonstrated significant responses of saproxylic beetle diversity to setting aside forest areas (Timonen *et al.*, 2011; Lassauce *et al.*, 2013). However, Horák, Chobot & Horáková (2012) raised the question of the status of the rare species pool, deeply affected by commercial forestry in European multisecular managed forests. In our study (Table 5), rare species were more abundant (but not more species-rich) in forest reserves than in managed plots (in agreement with previous results by Lassauce *et al.*, 2013 and Hardersen, 2003 in Germany). We therefore hypothesize (1) that set-aside areas may act as incubators for rare species found in neighboring managed areas, or (2) that forest management reduces the amount of habitats available to rare species and therefore their populations, without leading them to disappear or (3) that most rare species have disappeared and only populations of a few surviving species increase with the amount of dead wood. To address these questions, it would be helpful to use very old reserves as references for species distribution and abundance. Considering the short set-aside period in our study, saproxylic beetle assemblages were probably strongly influenced by both initial forest conditions (pre-existing large trees, beetle assemblages, etc.) and the spatial isolation of

the plots. The comparison between managed stands and set-asides should be deepened and a long-term monitoring strategy put in place (Djupström, Weslien & Schroeder, 2008).

Implications for forest management

Extended rotations, harvesting delays and reserves as conservation tools

In French forests, temporarily setting aside overmature stands before final harvesting, that is creating ageing and rotating islands (Lassauce *et al.*, 2013), is one of the management tools proposed to maintain saproxylic biodiversity associated with old successional stages. This approach aims to conciliate both timber production and biodiversity conservation goals. Larger trees generally have higher economic value while older stands have higher ecological value. We have shown that even a short delay in harvesting (minimum 30 years) induced significant changes in habitat conditions for saproxylic beetles, but only slightly affected saproxylic beetle assemblages. Further studies with longer harvesting delays would be necessary to analyze biodiversity responses. If longer-term habitat continuity is necessary for saproxylic beetle conservation, our results suggest that definitive strict fixed-location reserves should be favored over rotating and temporary set-asides. Moreover, the efficiency of ageing patches as temporary ecological sinks or sources has yet to be properly investigated.

Limits of management relinquishment and non-intervention: toward active restoration techniques?

Passive self-restoration of old-growth features through the abandonment of forest activities in harvestable deciduous stands takes time, at least for some features crucial for species conservation (large deadwood, tree microhabitats, etc.). Therefore, complementary active restoration techniques may be suggested to enhance the recruitment and accumulation of new substrates in conservation areas. Keeton (2006) showed that, in conventional silvicultural systems, active restoration is more successful in creating old-growth features than is delaying harvesting. For instance, standing dead trees, large downed deadwood and tree cavities can be artificially generated using cost-effective techniques like girdling trees, felling or pulling down large trees to be left on the forest floor and mechanically damaging tree trunks (with or without fungus inoculation). Costlier experiments with extreme habitat restoration have even been carried out in Italy (e.g. Cavalli & Donini, 2005). Active restoration requires an in-depth understanding of natural habitats to avoid structures inappropriate to local biodiversity; Jonsell, Nittérus & Stighäll (2004), for example, have underlined the differences between man-made and natural deadwood habitats. In any case, since most endangered saproxylic species have limited dispersal ability (e.g. Buse, 2012), the proper spatial distribution of created substrates is a prerequisite for effective restoration programs. The ecological impacts of active restoration techniques on biodiversity, but also on potential bark beetle outbreaks, should be monitored (Toivanen & Kotiaho, 2010). Thus said, active techniques should at least be considered when the restoration process must achieve the desired forest state within a relatively short time or when the species at stake are threatened by external factors.

Conclusions

Our results did not strongly support recommendations about extended rotations and reserve conservation in favor of saproxylic biodiversity. The rationale behind it would probably benefit from further studies in very old forest reserves, although they are scarce in Western Europe. In one of the study forests (Fontainebleau), despite a limited and unbalanced sampling design, we divided the class of L-UNH into old (> 30 years, $n = 3$) and very old (> 100 years, $n = 9$) reserves. From our exploratory analysis, the deadwood volume and diversity, the total beetle species richness, the rare species richness or abundance were not significantly higher in the older class. This trend deserves to be assessed by other case studies.

Forest areas left unharvested for more than 30 years show an accumulation of old-growth structures related to deadwood volumes and microhabitat diversity, but not deep changes in saproxylic beetle diversity. Restoring the old-growth-dependent community as a whole seems even slower than restoring these structural features. As suggested by Paillet *et al.* (2010), future work should examine the temporal effect of delayed harvesting at multiple time points on the same study area in order to evaluate, using a regression approach with the detailed time elapsed since harvesting, (1) how stands recover old-growth forest attributes and (2) how the associated saproxylic fauna colonize these set-asides in the long-term.

Acknowledgments

We are grateful to A. Lassauce, C. Moliard (Irstea), T. Barnouin, F. Soldati (ONF), N. Debaive (RNF) and all the local forest managers for field and laboratory work. We are indebted to Vicki Moore who reviewed the English manuscript, and to three anonymous reviewers whose constructive comments on an earlier version improved the manuscript. This research was granted by the French ministry in charge of the Ecology through the 'Biodiversité, Gestion Forestière et Politiques Publiques' (BGF) program (convention RESINE CVOJ 000 150, convention 10-MBGD-BGF-1-CVS-092, n°CHORUS 2100 214 651) and the National Forestry Board ('Office National des Forets', convention ONF-Cemagref, Action 5, 2008). This work was also partly funded by the French Environment and Energy Management Agency (ADEME).

References

Anderson, M.J. & Willis, T.J. (2003). Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* **84**, 511–524.

Aubry, K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., Woodard, B.L., Peterson, C.E., Lagoudakis, C.A. & Horton, A.J. (1999). Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO Study. *Northwest Sci.* **73**, 12–26.

Ball, J.P., Lindenmayer, D.B. & Possingham, H.P. (1999). A tree hollow dynamics simulation model. *For. Ecol. Manage.* **123**, 179–184.

Bauhus, J., Puettmann, K. & Messier, C. (2009). Silviculture for old-growth attributes. *For. Ecol. Manage.* **258**, 525–537.

Boncina, A. (2000). Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia. *Global Ecol. Biogeogr.* **9**, 201–211.

Bouget, C., Larrieu, L., Parmain, G. & Nusillard, B. (2013). In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodivers. Conserv.* **22**, 2111–2130.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*, Second edn: New York: Springer-Verlag.

Burrascano, S., Keeton, W.S., Sabatini, F.M. & Blasi, C. (2013). Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. *For. Ecol. Manage.* **291**, 458–479.

Buse, J. (2012). 'Ghosts of the past': flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. *J. Insect Conserv.* **16**, 93–102.

Calamini, G., Maltoni, A., Travaglini, D., Iovino, F., Nicolaci, A., Menguzzato, G., Corona, P., Ferrari, B., Di Santo, D., Chirici, G. & Lombardi, F. (2011). Stand structure attributes in potential old-growth forests in the Apennines, Italy. *Ital. For. Mount.* **66**, 365–381.

Cavalli, R. & Donini, F. (2005). Possible management actions to increase the amount of dead and marcescent wood, In *Deadwood: a key to biodiversity*: 100. Mason, F., Nardi, G. & Tisato, M. (Eds). Mantova: Sherwood, p.45–48.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrska, T. (2005). Deadwood in European beech (*Fagus sylvatica*) forest reserves. *For. Ecol. Manage.* **210**, 267–282.

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* **18**, 117–143.

Djupström, L.B., Weslien, J. & Schroeder, L.M. (2008). Deadwood and saproxylic beetles in set-aside and non set-aside forests in a boreal region. *For. Ecol. Manage.* **255**, 3340–3350.

Fan, Z., Shifley, S.R., Spetich, M.A., Thompson, F.R. & Larsen, D.R. (2005). Abundance and size distribution of cavity trees in second-growth and old-growth Central Hardwood Forests. *North J. Appl. For.* **22**, 162–169.

Fan, Z.F., Larsen, D.R., Shifley, S.R. & Thompson, F.R. (2003). Estimating cavity tree abundance by stand age and basal area, Missouri, USA. *For. Ecol. Manage.* **179**, 231–242.

Gibbons, P., McElhinny, C. & Lindenmayer, D.B. (2010). What strategies are effective for perpetuating structures provided by old trees in harvested forests? A case study on trees with hollows in south-eastern Australia. *For. Ecol. Manage.* **260**, 975–982.

Gotelli, N. & Colwell, R. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391.

Green, P. & Peterken, G.F. (1997). Variation in the amount of deadwood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. *For. Ecol. Manage.* **98**, 229–238.

Grove, S.J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* **33**, 1–23.

Hahn, K. & Christensen, M. (2004). Dead wood in European Forest Reserves – a reference for forest management. In *Monitoring and indicators of forest biodiversity in Europe – From ideas to operationality, EFI Proceedings No. 51*: 181–191. Marchetti, M. (Ed.). Joensuu: EFI.

Hanski, I. & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conserv. Biol.* **16**, 666–673.

Hardersen, S. (2003). Two lowland beech-oak forest areas abandoned for more than 30 years: what do bird and beetle communities tell us? In *Proceedings of the International Symposium: Deadwood: a key to biodiversity, Mantova, May 29th–31st 2003. Sherwood 95, Suppl. 2*: 33–36. Mason, F., Nardi, G. & Tisato, M. (Eds). Mantova: Sherwood.

Horák, J., Chobot, K. & Horáková, J. (2012). Hanging on by the tips of the tarsi: a review of the plight of the critically endangered saproxylic beetle in European forests. *Jour. Nature Conserv.* **20**, 101–108.

Jonsell, M., Nittérus, K. & Stighäll, K. (2004). Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. *Biol. Conserv.* **118**, 163–173.

Keeton, W.S. (2006). Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *For. Ecol. Manage.* **235**, 129–142.

Kirby, K.J., Webster, S.D. & Antczak, A. (1991). Effects of forest management on stand structure and the quantity of fallen deadwood: some British and Polish examples. *For. Ecol. Manage.* **43**, 167–174.

Lachat, T. & Bütler, R. (2009). Identifying conservation and restoration priorities for saproxylic and old-growth

forest species: a case study in Switzerland. *Environ. Manage.* **44**, 105–118.

Larjavaara, M. & Muller-Landau, H.C. (2010). Comparison of decay classification, knife test and two penetrometers for estimating wood density of coarse woody debris. *Can. J. For. Res.* **40**, 2313–2321.

Larrieu, L. & Cabanettes, A. (2012). Tree species and girth are key determinants for diversity and abundance of tree microhabitats in sub-natural montane beech-fir forests. *Can. J. For. Res.* **42**, 1433–1445.

Larrieu, L., Cabanettes, A. & Delarue, A. (2012). Impact of silviculture on deadwood and on the distribution and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. *Eur. J. For. Res.* **131**, 773–786.

Lassauce, A., Anselle, P., Lieutier, F. & Bouget, C. (2012). Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: a case study in French deciduous forests. *For. Ecol. Manage.* **266**, 273–285.

Lassauce, A., Larrieu, L., Paillet, Y., Lieutier, F. & Bouget, C. (2013). The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation length in French oak high forest. *Insect Conserv. Diver.* **6**, 396–410.

Lombardi, F., Lasserre, B., Tognetti, R. & Marchetti, M. (2008). Deadwood in relation to stand management and forest type in Central Apennines (Molise, Italy). *Ecosyst.* **11**, 882–894.

Marage, D. & Lemperiere, G. (2005). The management of snags: a comparison in managed and unmanaged ancient forests of the Southern French Alps. *Ann. For. Sci.* **62**, 135–142.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature* **405**, 243–253.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biol. Conserv.* **94**, 199–209.

Meyer, P. & Schmidt, M. (2011). Accumulation of deadwood in abandoned beech (*Fagus sylvatica* L.) forests in northwestern Germany. *For. Ecol. Manage.* **261**, 343–352.

Motta, R., Berretti, R., Castagneri, D., Lingua, E., Nola, P. & Vacchiano, G. (2010). Stand and coarse woody debris dynamics in subalpine Norway spruce forests withdrawn from regular management. *Ann. For. Sci.* **67**, 1–8.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G. & Ranius, T. (2003). Erratum to ''Densities of large living and dead trees in old-growth temperate and boreal forests''. *For. Ecol. Manage.* **178**, 355–370.

Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., de Bruyn, L., Fuhr, M., Grandin, U., Kana, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mézaros, I., Sebastia, M.-T., Schmidt, W., Standovar, T., Tothmérész, B., Uotila, A., Valladares, F., Vellak, K. & Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* **24**, 101–112.

Peterken, G.F. (1996). *Natural woodland: ecology and conservation in northern temperate regions*: Cambridge: Cambridge University Press.

Ranius, T., Niklasson, M. & Berg, N. (2009). Development of tree hollows in pedunculate oak (*Quercus robur*). *For. Ecol. Manage.* **257**, 303–310.

Rugani, T., Diaci, J. & Hladnik, D. (2013). Gap Dynamics and Structure of Two Old-Growth Beech Forest Remnants in Slovenia. *PLoS ONE* **8**, e52641.

Schmitt, C., Burgess, N., Coad, L., Belokurov, A., Besançon, C., Boisrobert, L., Campbell, A., Fish, L., Gliddon, D., Humphries, K., Kapos, V., Loucks, C., Lysenko, I., Miles, L., Mills, C., Minnemeyer, S., Pistorius, T., Ravilious, C., Steininger, M. & Winkel, G. (2009). Global analysis of the protection status of the world's forests. *Biol. Conserv.* **142**, 2122–2130.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *For. Ecol. Manage.* **128**, 211–225.

Sippola, A.-L., Siitonen, J. & Kallio, R. (1998). Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. *Scand. J. For. Res.* **13**, 204–214.

Sitzia, T., Trentanovi, G., Dainese, M., Gobbo, G., Lingua, E. & Sommacal, M. (2012). Stand structure and plant species diversity in managed and abandoned silver fir mature woodlands. *For. Ecol. Manage.* **270**, 232–238.

Timonen, J., Gustafsson, L., Kotiaho, J.S. & Mönkkönen, M. (2011). Are woodland key habitats biodiversity hotspots in boreal forests? CEE review 09-020 (SR81). Collaboration for Environmental Evidence: www.environmentalevidence.org/SR81.html

Toivanen, T. & Kotiaho, J.S. (2010). The preferences of saproxylic beetle species for different deadwood types created in forest restoration treatments. *Can. J. For. Res.* **40**, 445–464.

Vandekerkhove, K., De Keersmaeker, L., Baeté, H. & Walleyn, R. (2005). Spontaneous re-establishment of natural structure and related biodiversity in a previously managed beech forest in Belgium after 20 years of non intervention. *For. Snow Landsc. Res.* **79**, 145–156.

Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P. & Verschelde, P. (2009). When nature takes over from man: deadwood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. *For. Ecol. Manage.* **258**, 425–435.

Vanha-Majamaa, I. & Jalonen, J. (2001). Green tree retention in Fennoscandian forestry. *Scand. J. For. Res.* **16**, 79–90.

Vodka, S., Konvicka, M. & Cizek, L. (2009). Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *J. Insect Conserv.* **13**, 553–562.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**, 3–14.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Bouget *et al.* ACV-05–13-OM-091. Supplementary Material

Article 6: In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests

Biodivers Conserv (2013) 22:2111–2130
DOI 10.1007/s10531-013-0531-3

ORIGINAL PAPER

In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests

C. Bouget · L. Larrieu · B. Nusillard · G. Parmain

Received: 4 March 2013 / Accepted: 9 July 2013 / Published online: 23 July 2013

Abstract Deadwood-associated species are increasingly targeted in forest biodiversity conservation. In order to improve structural biodiversity indicators and sustainable management guidelines, we need to elucidate ecological and anthropogenic drivers of saproxylic diversity. Herein we aim to disentangle the effects of local habitat attributes which presumably drive saproxylic beetle communities in temperate lowland deciduous forests. We collected data on saproxylic beetles in 104 oak and 49 beech stands in seven French lowland forests and used deadwood, microhabitat and stand features (large trees, openness) as predictor variables to describe local forest conditions. Deadwood diversity and stand openness were consistent key habitat features for species richness and composition in deciduous forests. Large downed deadwood volume was a significant predictor of beetle species richness in oak forests only. In addition, the density of cavity- and fungus-bearing

C. Bouget (✉) · B. Nusillard · G. Parmain
National Research Institute of Science and Technology for Environment and Agriculture (Irstea), 'Forest Ecosystems' Research Unit, Domaine des Barres, 45290 Nogent-sur-Vernisson, France
e-mail: christophe.bouget@irstea.fr

B. Nusillard
e-mail: benoit.nusillard@irstea.fr

L. Larrieu
INRA, INPT/ENSAT/EIPURPAN, UMR 1201 Dynafor, 31326 Castanet-Tolosan, France
e-mail: Laurent.Larrieu@toulouse.inra.fr

L. Larrieu
Centre Régional de la Propriété Forestière de Midi-Pyrénées, 7 chemin de la Lacade, 31320 Auzeville Tolosane, France

G. Parmain
National Laboratory of Forest Entomology, National Forest Office (ONF), 2 rue Charles Péguy, 11500 Quillan, France

G. Parmain
Natural Patrimony Department, National Museum of Natural History, 36 rue Geoffroy St Hilaire, CP 41, 75 231 Paris Cedex 05, France

trees had weak but significant effects. We recommend that forest managers favor the local diversification of deadwood types, especially the number of combinations of deadwood positions and tree species, the retention of large downed deadwood and microhabitat-bearing trees in order to maximize the saproxylic beetle diversity at the stand scale in deciduous forests. To improve our understanding of deadwood-biodiversity relationships, further research should be based on targeted surveys on species-microhabitat relationships and should investigate the role of landscape-scale deadwood resources and of historical gaps in continuity of key features availability at the local scale.

Keywords Microhabitat · Deadwood · Forest management · Biodiversity indicator · Oak · Beech

Introduction

Deadwood is a key component of forest ecosystems that is among the most severely affected by management in many landscapes (Fridman and Walheim 2000) and has become a focal conservation target in sustainable management. Since deadwood is one of the most species-rich components in forest ecosystems (Grove 2002a), saproxylic species have become increasingly targeted in biodiversity conservation (Stokland et al. 2012). Deadwood has often been used as a structural indicator for naturalness and biodiversity and can provide information on the intensity of past human disturbances and degree of proximity to old-growth conditions (Larsson 2001). To help define ecologically-meaningful saproxylic-friendly practices for forest managers, we need to unravel the relative importance of ecological and anthropogenic drivers on saproxylic diversity.

Multiple factors play pivotal roles in predicting both the number and distribution of saproxylic species. Species assemblage composition may result from (i) macro-ecological features (distribution area, climate), (ii) environmental characteristics at the landscape scale and at the local scale, (iii) historical events (past disruption of substrate availability, local extinctions) and (iv) species interactions (competition, predation, interactive succession) (Stokland et al. 2012). Forestry practices act at the stand and the landscape scales. Therefore the understanding of variables driving biodiversity at the stand scale seems important to improve ecological sustainability of forestry.

Beetles are an important functional (Cobb et al. 2010) and numerical (20 % of all saproxylic species, just after the fungi; Stokland et al. 2004) component of saproxylic biodiversity. Since beetles belong to relatively well-known taxonomic groups, and since most species are highly sensitive to environmental changes, have specific habitat demands and can be trapped relatively easily, they are both logistically and ecologically suitable as response indicators (Siitonen 2001).

At the local (stand) scale, habitat quality for saproxylic beetles is related to abiotic conditions (e.g. moisture and temperature conditions related to canopy closure) and available resources. Resources not only include deadwood substrates, but also more cryptic biological legacies such as microhabitats (e.g. cavities, crown deadwood), mostly found in large-diameter live trees (Larrieu and Cabanettes 2012; Winter and Möller 2008). Density and/or diversity of resources may underlie the resource-biodiversity relationship. Forest stands with a wider range of resources (resource range hypothesis) and/or a higher density of substrates (resource concentration hypothesis) may be able to support a larger number of

species due to demographic, stochastic and dispersal processes affecting local population dynamics (Päivinen et al. 2003). Several studies have demonstrated a positive significant correlation between the local amount of deadwood and saproxylic beetle species richness (see Grove 2002a). Nevertheless, in a meta-analysis of available European data, Lassauce et al. (2011) found only a weak relationship between deadwood volume and species richness in temperate forests. Moreover, several studies have shown the diversity of deadwood types, rather than mere deadwood quantity, to be a critical environmental variable for saproxylic beetles (e.g. Brin et al. 2009; Stokland et al. 2004).

During the last few decades, research on saproxylic beetle habitat associations has been common in Scandinavia (Stokland et al. 2012), but has received less attention in central, western and southern Europe. By expanding this research to oak and beech forests, the two main deciduous forest types in Europe, we aimed to better understand the surrogacy patterns and environment-biodiversity relationships found there and to determine (i) relevant structural indicators of saproxylic beetle diversity and (ii) improved guidelines for sustainable forest management. We here mainly intended (i) to disentangle the effects of local habitat attributes (abiotic conditions, density or diversity of resources) which presumably drive saproxylic beetle communities in deciduous forests, and (ii) check whether key habitat features for saproxylic beetles are consistent over oak and beech forests.

Materials and methods

Study areas

We collected environmental and entomological data using standardized protocols on 153 plots in seven lowland deciduous forests (Table 1), distant of several hundred kilometers from each other: one forest in western France (Chize), three in eastern France (Auberive, Citeaux, Combe-Lavaux), one in central France (Troncais) and two in northern France (Rambouillet, Fontainebleau). Two forest types were distinguished—oak and beech—according to the dominant tree species in terms of basal area. All the beech stands were associated with oak stands in the vicinity. Highland beech forests have been studied in a companion study. Inside each forest, plots were distant of hundreds of meters from each other and half of the plots were located in protected forest reserves (except in the Rambouillet and the Troncais forest, where only 20 and 10 % were in reserve stands, respectively).

Beetle sampling and identification, species characterization

Flying saproxylic beetles were sampled with two cross-vane flight interception traps (Polytrap^{TM}) per plot, set about 20 m from each other, for a total number of 306 traps. The traps were suspended roughly 1.5 m above the ground. Active insects were collected from April to August, during 1 year only. The following saproxylic taxa were not identified at the species level in at least one of the seven forests and therefore removed from the compiled dataset: Cryptophagidae, Ptiliidae, Staphylinidae incl. Scaphidiinae and Pselaphinae. For the other taxa, we characterized each species' degree of geographic rarity in France according to the FRISBEE database (Bouget et al. 2010) and distinguished common (abundant and/or widely distributed) and rare (not abundant and only locally distributed) species of conservation concern for specific analyses.

Table 1 Description of structural (deadwood, microhabitats, large trees, openness, forest type) variables and study sites explored in the study

		Beech		Oak	
		Mean ± SE	Range	Mean ± SE	Range
Deadwood	Total volume of deadwood in a 0.3 ha plot (m^3/ha)	66.561 ± 11.771	0–371	28.131 ± 2.676	0–123
	Volume ratio = deadwood/(Live trees + deadwood)	0.213 ± 0.031	0–1	0.107 ± 0.009	0–0.5
	Nb deadwood types (tree species × diameter × decay × position)	10.122 ± 0.816	1–28	19.971 ± 1.254	1–53
	Volume of standing deadwood (>10 cm in diameter) in a 0.3 ha plot (m^3/ha)	18.284 ± 4.357	0–128	4.886 ± 0.922	0–65
	Volume of large standing deadwood (>40 cm in diameter)) in a 0.3 ha plot (m^3/ha)	14.705 ± 4.336	0–128	2.801 ± 0.818	0–65
	Volume of downed deadwood (>10 cm in diameter) in a 0.3 ha plot (m^3/ha)	48.277 ± 8.953	0–287	20.657 ± 2.379	0–111
	Volume of large downed deadwood (>40 cm in diameter) in a 0.3 ha plot (m^3/ha)	21.537 ± 5.698	0–209	4.2 ± 1.186	0–101
Microhabitat	Total density of microhabitat-bearing trees in a 1 ha plot	16.918 ± 1.744	0–52	17.663 ± 1.031	3–50
	Number of microhabitat types in a 1 ha plot	4.469 ± 0.260	0–7	4.779 ± 0.135	1–7
	Density of cavity-bearing trees in a 1 ha plot: "empty" cavities with an entrance above 3 cm in width, woodpecker breeding and feeding holes, deep cavities formed between roots, cavities with mould with an entrance above 10 cm in width	7.612 ± 0.713	0–18	5.558 ± 0.396	0–20
	Density of fungus-bearing trees in a 1 ha plot: fruiting bodies of tough or pulpy saproxylic fungi, >5 cm in diameter,	1.306 ± 0.238	0–7	0.942 ± 0.115	0–7
	Density of deadwood-bearing trees a 1 ha plot: crown deadwood in (large dead branches >20 cm in diameter and >1 m in length, crown deadwood volume >20 % of the total crown wood volume)	6.02 ± 1.052	0–37	8.096 ± 0.742	0–31
	Density of sap-run-bearing trees: sap runs >10 cm in length in a 1 ha plot	0.286 ± 0.071	0–2	0.423 ± 0.083	0–4

Table 1 continued

		Beech		Oak	
		Mean ± SE	Range	Mean ± SE	Range
Large trees	Number of very large trees in a 1 ha plot (dbh > 67. 5 cm)	4.816 ± 1.035	0–32	12.25 ± 1.181	0–51
	Basal area of very large trees in a 0.3 ha plot ($67.5 < dbh \leq 87.5$ cm) (m^2/ha)	1.768 ± 0.481	0–15	5.611 ± 0.602	0–30
	Basal area of the largest trees in a 0.3 ha plot (dbh > 87.5 cm) (m^2/ha)	0.982 ± 0.361	0–14	0.753 ± 0.208	0–12
Openness	Open areas (clearings, edges, areas with a well developed herb layer composed of flowering plants) (%) in a 1 ha plot	10.792 ± 2.883	0–100	15.228 ± 2.734	0–100
	Beech or oak	49 plots, 98 traps		104 plots, 208 traps	
Forests	Auberive (AUB)	15 plots, 30 traps		9 plots, 18 traps	
	Chize (CHZ)	12 plots, 24 traps		12 plots, 24 traps	
	Citeaux (CIT)			12 plots, 24 traps	
	Combe-Lavaux (CL)	5 plots, 10 traps		3 plots, 6 traps	
	Fontainebleau (FBL)	17 plots, 34 traps		7 plots, 14 traps	
	Rambouillet (RBT)			30 plots, 60 traps	
	Troncais (TR)			31 plots, 62 traps	

Live tree and deadwood measurements

Stands were surveyed to obtain estimates of wood volumes for live trees, snags, logs and stumps and the basal area of live trees. Each plot, centered in the middle of both traps, was approximately 0.3 ha in size. We used a combination of sampling methods: fixed-angle relascope or circular plots for live trees; circular plots for stumps, large snags and large logs; line intersect sampling for small logs. We took into account minimum diameters of 7.5 cm for live trees, snags and logs. Four variables were used to describe deadwood: tree species, diameter (6 classes from 5 to >70 cm), decay stage (9 classes created by crossing 3 classes of remaining bark cover and 3 classes of inner wood hardness assessed by "knife penetration test"; Larjavaara and Muller-Landau 2010), and position (downed, standing, stump). An index of deadwood diversity was calculated as the number of observed deadwood types, i.e. the number of combinations of the above four variables (tree species × diameter class × decay class × position), as suggested by Siitonen et al. (2000). We also figured out a Shannon deadwood diversity index (Dodelin et al. 2004), accounting for the individual density (i.e. its number of pieces), and not only the occurrence, of each deadwood type. Based on these surveys, seven deadwood variables were considered for analysis (Table 1): (i) total volume, (ii) volume ratio, (iii) number of deadwood types, (iv) volume of standing deadwood, (v) volume of large standing deadwood (>40 cm in mid-diameter), (vi) volume of downed deadwood, (vii) volume of large downed deadwood (>40 cm in mid-diameter).

The basal area of very large and largest live trees was calculated for each 0.3 ha plot. The thresholds defining large trees were given by Grove (2002b), Larrieu and Cabanettes (2012) and Nilsson et al. (2002).

Very large live trees ($67.5 < \text{dbh} \leq 87.5$ cm) and tree microhabitats were inventoried during leaf-out in 1 ha circular plots centered around the two traps. We recorded seven microhabitat types borne by live trees: (i) "empty" cavities, (ii) cavities with mould, (iii) fruiting bodies of saproxylic fungi, (iv) sap runs, (v) dead branches, (vi) tree crown deadwood, (vii) missing bark (i.e. hard patches of wood with no bark >600 cm^2). Microhabitats other than crown deadwood were only recorded when visible on the trunk beneath and within the tree crown. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type. The total density of microhabitat-bearing trees, the number of microhabitat types and the individual densities of four microhabitat types (i)"empty" and mould cavities, ii) sporocarps of saproxylic fungi, iii) dead branches and tree crown deadwood and iv) sap runs) were considered for analysis. Stand openness was defined as the total proportion of open areas in a 1 ha plot.

Data analysis

We used deadwood, microhabitat and stand features as predictor variables to describe forest conditions (Table 1), and species richness of *rare* and *common* species and species composition (incl. singletons) as response variables to describe beetle assemblages. All analyses were conducted on oak and beech datasets with R software v. 2.12.0. Since the same set of environmental variables measured within the 0.3- and 1 ha plots was used for both traps in the same plot, the catches of these two traps were combined prior to analyses carried out at the *plot* level.

To rank the effects of environmental variables on variations in species composition, we performed a Canonical Analysis of Principal Coordinates (*vegan* R-package, CAP,

Anderson and Willis 2003). From Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, since co-linearity among predictor variables is not considered to be a problem in CAP (Anderson and Willis 2003). We calculated total constrained inertia, the constrained inertia which was not explained by spatial factors only (NSCI), the total (intrinsic + co-explained) inertia explained by each variable (after partialling out the geographical "*forest*" effect), the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance by means of permutation tests (100 runs), and the relative contribution of each variable to NSCI.

We assessed the multi-model-averaged estimates (Burnham and Anderson 2002) determining the response of species richness to stand features. The most parsimonious model had the lowest Akaike information criterion (AICc, Burnham and Anderson 2002). For each response variable, we generated the null model and models with all the valid combinations of two explanatory variables. We calculated the differences in the AICc scores between each model and the best model (ΔAICc) as well as the Akaike weights for each model. All models with $\Delta AICc < 2$ were used in order to figure out the model-averaged estimates weighted by the model weights. Only significant variables ($p < 0.05$ across all the models) were selected; their relative contribution, i.e. their weight of evidence across all the models, was indicated (*lme4*, *MuMIn*, *arm* R-packages). Since co-linearity among predictor variables may lead to unreliable parameter estimates, we conducted the strategy suggested by Zuur et al. (2010) for addressing the multicolinearity problem before model averaging. We sequentially dropped the covariate with the highest variance inflation factor (VIF), then recalculated the VIF and repeated this process until all VIFs were below a pre-selected threshold (Zuur et al. (2010) suggest a cutoff of 3). The VIF represents the proportion of variance in one predictor explained by all the other predictors in the model; a VIF = 1 indicates no co-linearity, whereas increasingly higher values suggest increasing multicolinearity. We used the "vif.mer" function (Frank 2011) to calculate VIFs for linear mixed effects models built using the lmer function in the "lme4″ package (Table 2). Since the relationship between species richness and deadwood volumes is better described by semi-log models (Martikainen et al. 2000), we used (log x + 1) transformed values for deadwood volumes. The effect on species richness of local deadwood diversity assessed by the simple index (number of deadwood types) or the Shannon index (Shannon diversity index of deadwood types, taking the local density of each deadwood type into account, using its number of pieces) was compared using AICc values of each mixed model (with forest as a random factor).

Significant relationships in generalized linear models were searched for breakpoints in species accumulation rates. Estimates of breakpoints were calculated by recursive partitioning by means of maximally selected two-sample statistics (Hothorn et al. 2006). Only primary and significant ($p < 0.001$) breakpoints are reported here. Based on 5,000 bootstrap samples, 80 % confidence intervals (to define ranges more tightly than 95 % CI) were calculated for all breakpoints (*party* and *boot* R-packages). In comparison with other models used in the study, this method does not allow to take the spatial structure of the data (at least forest location) into account.

The diversity effect was partitioned into its four basic dimensions included in the deadwood diversity index (diameter class, decay class, tree species, position). We analysed whether any of these dimensions have an outstanding importance on species richness, by comparing AICc values of linear mixed models (with forest as a random factor) including all combinations of the 4 deadwood dimensions.

Table 2 Variance inflation factor (VIF) of predictor variables selected in the linear mixed reduced models of species richness (with forest as a random effect), to be used in the model averaging approach (after sequential selection; Zuur et al. 2010), for addressing the multicollinearity problem

Predictor (covariate)	Oak	Beech
Deadwood diversity	2.26	2.24
Deadwood ratio		2.33
Volume of standing deadwood (logx + 1)	2.79	2.41
Volume of large standing deadwood (logx + 1)	2.70	
Volume of downed deadwood (logx + 1)	2.26	
Volume of large downed deadwood (logx + 1)	1.77	
Density of very large trees	1.71	
Basal area of largest trees	1.99	1.70
Density of cavity-bearing trees	2.34	2.34
Density of fungus-bearing trees	1.82	1.74
Density of deadwood-bearing trees	1.46	1.61
Density of sap-run-bearing trees	1.47	1.64
Microhabitat diversity	2.33	
Openness	1.41	1.53

The VIF represents the proportion of variance in one predictor explained by all the other predictors in the model. A VIF = 1 indicates no collinearity. All selected VIFs were below a pre-defined cutoff of 3 (as suggested by Zuur et al. 2010)

The response to stand openness of the abundance of selected beetle species (caught in more than 10 individuals occurring in more than 10 % samples) was analyzed using a Generalized Linear Mixed Model with a Poisson error distribution, and "forest" as a spatial random effect (lmer function in lme4 R-package).

Results

Overall, the compiled dataset included 99 383 individuals and 478 saproxylic beetle species, among which 377 common, 70 rare (15 % of the total number) and 31 undefined species were recorded. On average per plot, rare species represented about 6 % of all species and 6 % of all individuals. The mean numbers of common and rare species per plot were greater in the oak than in the beech plots (49.7 ± 1.7 vs. 38.1 ± 1.9 and 3.5 ± 0.2 vs. 1.9 ± 0.1, respectively). Significant differences in several explanatory stand features were measured between oak and beech plots (Table 1).

Response of species composition to stand features

Many factors were used to describe the saproxylic environment (deadwood, microhabitats, large trees, stand openness) in order to identify the main local factors driving saproxylic beetle diversity. In oak and beech data, environmental and spatial factors respectively accounted for 45 and 52 % of variation in species composition. 31 and 23 % of the constrained inertia was explained by the intrinsic site effect in oak and beech data.

In oak and beech forests, the openness, the microhabitat diversity, the deadwood diversity and the basal area of very large trees made significant total contributions

(marginal and joined) to inertia (Table 3). In the oak forests, microhabitat density also provided a significant total contribution. In the beech forests, significant total contributions were also provided by all the other deadwood descriptors (total volume, ratio, volumes of standing, large standing, downed, large downed deadwood), the density of very large trees at the 1 ha scale and the basal area of the largest trees. In oak, two environmental variables (deadwood diversity and stand openness) had a significant marginal contribution to inertia but only explained 3.5 and 3.9 % of the non-spatial constrained inertia, respectively. In beech data, although a larger proportion of the inertia was explained by the environmental predictors than in oak data, none of the tested environmental predictors made a significant intrinsic contribution to inertia. In beech and oak forests, the density of cavity-, fungus-, deadwood-, sap-run-bearing trees did not explain variations in species composition.

Response of species richness to stand features

From multi-model averaged estimates (Table 4), the stand openness was the main predictor of richness of common beetle species in oak and beech plots. The deadwood diversity and the density of fungus-bearing trees had the highest positive impacts on rare species richness in oak and beech forests, respectively. The more open the forest and the higher the local number of deadwood types, the higher the number of common species per plot in beech and oak forests, and the number of rare species in oak stands. In oak stands, the number of common species also significantly increased with the volume of all downed deadwood (the second best predictor after openness), and to a lesser extent, with the volume of large downed deadwood, and with the density of fungus- and cavity-bearing trees. Overall, the influential stand features were only partially identical for rare and common species. The influence of the total volume of deadwood on the number of species was not tested, since it was collinear with other predictors in the model (Table 2).

Above the identified deflation breakpoints for significant variables, the number of species per plot kept on increasing, but more slowly. The rate of increase in rare species richness slightly slows down after the value of 1 fungus-bearing tree per ha in beech forests, and after the value of 29 deadwood types in the surrounding 0.3 ha in oak forests. The accumulation rate of common species slows down after a 17 % openness in oak stands and a 2 % openness in beech stands. In oak forests, the number of common species increased more slowly after the values of 11 deadwood types in the surrounding 0.3 ha, 1 fungus-bearing tree per ha, 46 m^3 of downed deadwood per ha.

In both beech and oak plots, the effect of deadwood diversity on species richness was partitioned into its four basic dimensions (diameter, tree species, decay, position [i.e. downed, standing or stump]). We did not measure any sharp contrasts between AICc values of linear mixed models including all combinations of the 4 deadwood dimensions for common and rare species (Fig. 1). The full model was never the most parsimonious model. The best model included (i) the number of combinations between positions and tree species, and to a lesser extent simply the diversity of deadwood positions ($\Delta AICc = 1$) for rare and common species in beech forests, (ii) the diversity of tree species, and to a lesser extent of diameter classes $\Delta AICc = 2$) for rare species and (iii) the number of combinations crossing tree species, diameter and decay stages for common beetle species in oak forests. Although the most structuring deadwood dimensions for species richness were not strictly consistent between oak and beech, and between common and rare species, the number of tree species was generally outstanding (Fig. 1).

Table 3 Canonical analysis of principal coordinates (CAP) used to partition the variation in the response species-plot matrix with respect to the combination of explanatory stand features (deadwood, microhabitat, large trees, openness); %NSCI: relative contribution to the non-spatial constrained inertia

		Oak plots			Beech plots		
	Variable	Total inertia	Marginal Inertia	%NSCI	Total inertia	Marginal Inertia	%NSCI
Deadwood	Volume of deadwood (logx + 1)	ns			0.589*	ns	
	Deadwood ratio	ns			0.529**		
	Deadwood diversity	0.481**	0.406*	3.5 %	0.465*		
	Volume of standing deadwood (logx + 1)	ns			0.591**		
	Volume of large standing deadwood (logx + 1)				0.548*		
	Volume of downed deadwood (logx + 1)				0.582*		
	Volume of large downed deadwood (logx + 1)				0.664*		
Microhabitat	Microhabitat density	0.404*	ns		ns	ns	
	Microhabitat diversity	0.485*			0.453°		
Large trees	Basal area of very large trees	0.420*	ns		0.723**	ns	
	Density of very large trees	ns			0.592**		
	Basal area of largest trees				0.761**		
Openness	Openness	0.663**	0.445*	3.9 %	0.513**	ns	
Spatial	Forest	11.415**	5.120**		3.392**	2.181**	

Only significant variables (** $0.01 > p > 0.001$, * $0.05 > p > 0.01$, °$0.1 > p > 0.05$) were selected

Table 4 Multi-model averaged estimates for structural stand features (deadwood, microhabitats, large trees, openness) determining the response of saproxylic beetle species richness (rare, common)

Forest type	Species richness	Predictor	Model-averaged estimate (significance)	Relative contribution	Deflation breakpoint	Best models (Delta AICc < 3)	
Oak	Rare	Deadwood diversity	1.66**	0.81	29 (19–30)	Deadwood diversity + openness	AICc = 421.1
		Openness	0.81*	0.34	No		
	Common	Openness	9.0***	0.99	17 (3–80)	Volume of downed deadwood + openness	AICc = 767.9
		Volume of downed deadwood (logx + 1)	9.4***	0.94	46 (12–47)		
		Volume of large downed deadwood (logx + 1)	7.7***	0.04	No		
		Deadwood diversity	10.0**	0.01	11 (10–17)		
		Density of fungus-bearing trees	5.4**	0.01	1 (1–3)		
		Density of cavity-bearing trees	4.3°	0.01	No		
Beech	Rare	Density of fungus-bearing trees	1.09*	0.56	1 (1–3)	Density of fungus-bearing trees	AICc = 181.5
	Common	Openness	14.38***	0.97	2 (1–10)	Deadwood diversity + openness	AICc = 378.0
		Deadwood diversity	6.27°	0.24	No		

Relative importance is the weight of evidence for each parameter across all the best models combining several variables (mixed-effect models, with forest as a random effect). Only significant variables (*** $p < 0.001$, ** $0.01 > p > 0.001$, * $0.05 > p > 0.01$, °$0.1 > p > 0.05$) were selected. Significant relationships in SR response were searched for breakpoints (Significance $p < 0.001$, 80 % Confidence Interval based on 5,000 bootstrap samples)

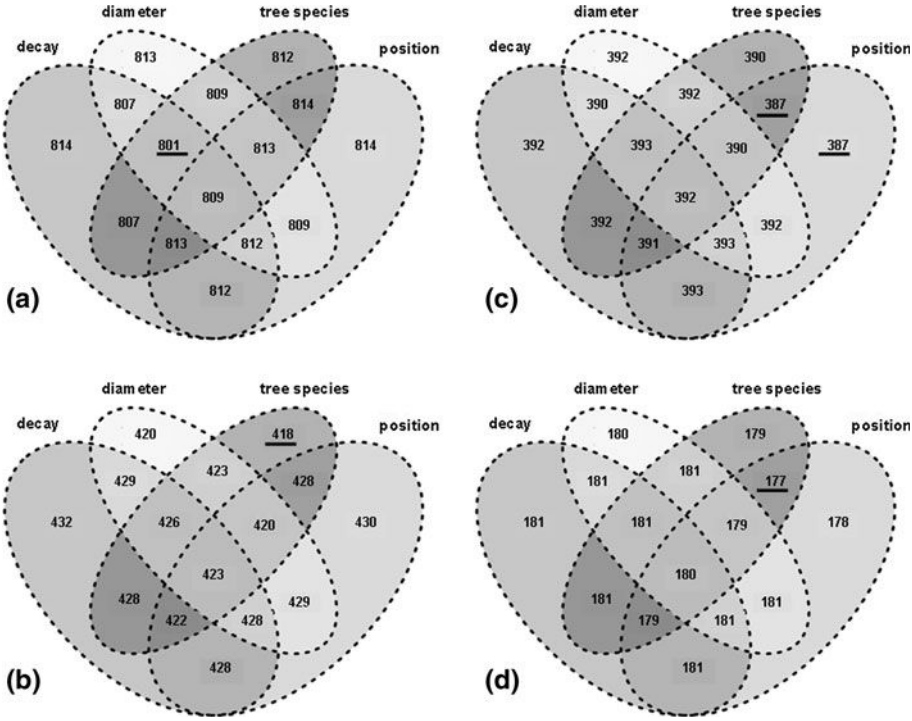


Fig. 1 Partitioning of the deadwood diversity effect on common and rare species richness into its four basic dimensions (diameter class, decay class, tree species, position) and all their combinations in beech and oak plots. All mixed models (with forest as a random factor) for all combinations of the 4 deadwood properties were compared using AICc values. The four-set Venn diagram with simple ellipses displays all 24-1 = 15 possible areas created by the interaction of 4 sets. The Venn diagram was not scaled, i.e. the graphical size of each intersecting or non-intersecting area is not proportional to the numerical AICc value. The best model is underlined. **a** and **b**: oak forests, **c** and **d**: beech forests; **a** and **c**: common species, **b** and **d**: rare species

Both deadwood diversity indices, the simple number and the Shannon diversity index of deadwood types, were similarly correlated to the deadwood volume (Spearman rho = 0.48 for the simple index, rho = 0.49 for the Shannon index). In both beech and oak data, the explanatory power of the Shannon model was only slightly better than the simple model (ΔAICc = 4).

Response of individual species to openness

30 and 36 % of tested species (102 species in beech stands, 189 species in oak stands) had a significant response to openness in beech and oak data, respectively (Table 5). In both beech and oak data, 77 % of the significant species responses related to open-preferring species, and only 23 % to shade-preferring taxa (whose abundance decreased with increasing stand openness). Among open-preferring species, 30 % species were known to have flower-visiting adults. Contrarily, we did not find any known flower-visiting species among shade-preferring taxa. Only a few species displayed contrasting responses to openness in oak and beech data (Table 5).

Table 5 Response in abundance of selected beetle species to stand openness

Shade-preferring species		Open-preferring species	
Oak stands	Beech stands	Oak stands	Beech stands
*Anobium hederae****, *Hemicoelus fulvicornis****, *Isoriphis melasoides****, *Leiopus femoratus****, *Melasis buprestoides**, *Mycetophagus piceus**, *Ochina ptinoides**, *Orchesia undulata**, *Pediacus dermestoides****, *Tetratoma ancora****, *Vincenzellus ruficollis****, *Xyleborinus.saxesenii****	*Aulonothroscus brevicollis**, *Diplocoelus fagi**, *Platystomos albinus**	*Abdera bifasciata***, *Agrilus* sp***, *Alosterna tabacicolor**, *Ampedus cinnaberinus**, *Ampedus sanguinolentus***, *Anaspis fasciata**, *Anaspis frontalis****, *Anaspis melanopa****, *Cis boleti***, *Clerus mutillarius****, *Clytus arietis**, *Colydium elongatum****, *Cortinicara gibbosa****, *Cortodera humeralis****, *Cryptarcha undata****, *Cryptolestes duplicatus***, *Dasytes aeratus***, *Dasytes plumbeus****, *Dryocoetes villosus****, *Epuraea* sp***, *Gonodera luperus****, *Megatoma undata***, *Mycetochara maura****, *Mycetophagus atomarius**, *Pachytodes cerambyciformis**, *Paromalus parallelepipedus**, *Pediacus depressus**, *Placonotus testaceus****, *Plegaderus dissectus***, *Prionus coriarius***, *Ptinus bidens****, *Ptinus subpilosus**, *Rhagium sycophanta***, *Rhizophagus bipustulatus**, *Rhizophagus depressus****, *Silvanus unidentatus**, *Stenurella melanura****, *Thanasimus formicarius****, *Triplax lepida**, *Tritoma bipustulata****, *Tropideres albirostris****, *Xyleborus dryographus****	*Ampedus glycerus****, *Corticarina similata**, *Cyclorhipidion bodoanus****, *Enicmus brevicornis****, *Glischrochilus quadriguttatus**, *Laemophloeus monilis****, *Leptura aurulenta***, *Melanotus villosus**, *Microrhagus lepidus****, *Nemozoma elongatum****, *Platycerus caraboides***, *Stenocorus meridianus****, *Tomoxia bucephala****
*Hemicoelus costatus***, *Trypodendron domesticum***, *Xyleborus dispar****, *Xylosandrus germanus****		*Cerambyx scopolii****, *Cetonia aurata****, *Cryptarcha strigata****, *Dacne bipustulata****, *Litargus connexus****, *Pyrochroa coccinea***, *Scolytus intricatus****, *Taphrorychus bicolor****, *Triplax russica****, *Valgus hemipterus***, *Xyleborus monographus****	

Table 5 continued

Shade-preferring species		Open-preferring species	
Oak stands	Beech stands	Oak stands	Beech stands
Species with contrasting response in oak and beech data			
*Microrhagus pygmaeus**	*Hylecoetus dermestoides***	*Hylecoetus dermestoides****	*Microrhagus pygmaeus****
*Isoriphis marmottani****			*Ernoporicus fagi****
*Salpingus planirostris****			*Isoriphis marmottani****
*Ernoporicus fagi****			*Salpingus planirostris***

Only species caught in more than 10 individuals and occurring in more than 10 % samples were analyzed using a Generalized Linear Mixed Model with a Poisson error distribution, and "forest" as a spatial random effect. Only significant responses were displayed (*** $p < 0.001$, ** $0.01 > p > 0.001$, * $0.05 > p > 0.01$). Species with well-known flower-visiting adults (Bouget et al. 2010) were underlined

Discussion

Local ecological drivers of saproxylic beetle diversity in temperate deciduous forests

Stand openness, a key feature

To summarize, among the diverse features describing local forest conditions for saproxylic beetles, both deadwood diversity and stand openness were consistent key habitat features for species richness and composition in oak and beech forests. The more open the deciduous forest, the higher the number of common species per plot in beech and oak forests, and the number of rare species in oak stands. Variations in species composition were mainly determined by the openness and the deadwood diversity in the oak plots, by site and large tree predictors in the beech plots. Moreover, a high proportion of the tested species displayed a significant response to openness (30 and 36 % in beech and oak data, respectively). Our study confirms that canopy closure is clearly an outstanding attribute of the surrounding environment for saproxylic (even rare) beetles (Stokland et al. 2012). We here observed the same high proportion (77 %) of open-preferring species among significant species responses in oak and beech forests. This strong influence of openness on both species richness and composition could relate (i) to an ecological complementation effect, between neighboring deadwood for larvae and flowers for adults, (ii) to microclimatic effects on sun-exposed substrates (and therefore habitat suitability of deadwood, fungi and other microhabitats on trees), as demonstrated in temperate forests by Vodka et al. (2009), and (iii) to thermodynamic effects on beetle activity, with more flying-active species in open and sun-exposed environments. Concerning the first point, we respectively detected 30 and 0 % flower-visiting species among open- and shade-preferring taxa. Our analyses also indicated that the accumulation rate of common species slows down after a 17 % openness in oak stands and a 2 % openness in beech stands. Contrary to what we had expected, we did not observe humpback curves with two breakpoints, i.e. a decrease in richness after a second breakpoint due to the disappearance of species in extreme sun-, wind- and light-exposed substrates. The potential influence of a trappability bias (window-flight traps may be more efficient in open areas) has not been elucidated (Koch Widerberg et al. 2012).

Density and diversity of deadwood

Overall, deadwood diversity was actually a more consistent predictor of species richness than deadwood ratio and downed or standing deadwood volumes. Its co-linearity with the total deadwood volume (Spearman correlation = 0.49) prevents from disentangling their relative effects. The deadwood diversity significantly affected the species richness in beech and oak forests (as well as the species composition in oak forests). In other words, the higher the local number of deadwood types, the higher the number of common species per plot, and the number of rare species in oak stands. Our overall results confirm that the diversity of deadwood substrates plays an outstanding role in saproxylic diversity, as several previous studies have shown (e.g. Brin et al. 2009; Økland et al. 1996; Stokland et al. 2004). A wider range of resources (i.e. more various types of resource present in exploitable amounts) hosts more specialists and as many generalist species. Among the 4 dimensions describing deadwood diversity (position, decay, diameter, tree species), the local number of (deciduous) tree species was a key element for species richness.

The deadwood ratio (the proportion of deadwood in total local wood volume, alive and dead), accounting for the wide natural variability in deadwood amounts over space and time due to the productivity of the forest and stand dynamics (Siitonen 2001), did not better fit the relationship between deadwood amount and species richness than absolute deadwood volume.

Some studies have pointed out that the decline in deadwood quantity due to commercial forestry is stronger for some deadwood types, mainly snags and large logs (Sippola et al. 1998). These two components are therefore particularly at risk in managed forests. It has already been shown that oak and beech snags (Bouget et al. 2012; Brunet and Isacsson 2009) and large logs (Brin et al. 2011; Økland et al. 1996) are key deadwood types for saproxylic beetles. In our study, the volumes of downed and standing deadwood did not provide significant intrinsic contributions to assemblage composition in oak and beech plots. The best models of species richness in lowland forests never included the standing deadwood. However, it should be noted that, in a companion study (Bouget et al., in prep.), the density of large standing deadwood was the second predictor of species richness in highland beech forests. Deadwood drivers clearly depend on the forest context.

In oak stands, the number of common species also significantly increased with the volume of all downed deadwood (the second best predictor after openness), and to a lesser extent, with the volume of large downed deadwood, both being even more influent than the deadwood diversity. Large deadwood volume did not affect the number of rare species, even though certain rare species are known to be sensitive to large log volume (Siitonen et al. 2000). Possibly the threshold we set for large deadwood (>40 cm), given for boreal forests by Nilsson et al. (2002), was too low to reflect ecological processes or should be modified for temperate contexts. Possibly species depending on large logs might be simply missing in managed forests due to the scarcity of large deadwood pieces.

Tree microhabitats as key resources?

In addition to canopy closure and deadwood resources; microhabitat features, as newly studied features, had weak but significant effects. The number of common species in oak stands and rare species in beech forests significantly increased with the density of fungus-bearing trees. Moreover the density of cavity-bearing trees had a slight positive impact on the common species richness in oak stands. However, in beech and oak forests, the density of cavity-, fungus-, deadwood-, sap-run-bearing trees did not explain variations in species composition. The role of tree microhabitats for saproxylic assemblages remains

insufficiently understood (Winter and Möller 2008). Several saproxylic beetle species are known to be associated to cavities and tree holes (Ranius 2002), to sap runs (Yoshimoto et al. 2005), to crown deadwood (Bouget et al. 2011) and lignicolous fungi (Jonsell and Nordlander 2002). Microhabitats borne by live trees can occur in forests with a low total amount of deadwood. In our data, the density and diversity of microhabitats on trees and deadwood were not correlated.

Grove (2002b), Nilsson et al. (2002) and Ranius (2002) all suggested that the density of large trees could be important for certain saproxylic beetle species, since the presence of such trees reflects both habitat continuity and microhabitat supply. In our dataset, the density of large trees actually only correlated to the density of deadwood-bearing trees, but not to the density of cavity-, of fungus- and of sap-run-bearing trees. In our results, the density or basal area of large or very large trees did not explain local species richness either at a 0.3 ha scale or at a 1 ha scale. Nevertheless, variations in species composition were co-determined by site and large tree predictors in the beech plots.

The weak relationships observed between microhabitats and beetle fauna may be attributed to deficiencies (i) in beetle sampling and/or (ii) in the microhabitat surveys, and (iii) to the strong co-linearity among microhabitat variables in the modeled data. In beech data multiple joint effects between close variables or between environmental and spatial variables, made it difficult to decipher influences. In interpreting the results, we consequently should bear in mind that the present samples enable to reveal only strong effects. First, our beetle dataset is based on two window-flight traps per plot, set up during 1 year only. However, it has been demonstrated that the number of species detected at the plot level could be deeply increased by year or trap replication (Parmain et al. in press). Since the sampled assemblage may be poorly representative of the local fauna, it may weaken the analysis of the species-environment relationships. Moreover, it should be underlined that freely hanging window-flight traps are meant to catch active flying beetle species, and that (mostly rare) microhabitat-specialists, e.g. cavity-specialists, are only occasionally caught in these traps, unless a large sample size is set up. To study these groups, special kinds of targeted surveys or trapping methods are needed (Ranius and Jansson 2002). Our conclusions regarding rare species should be considered cautiously, since it is well known that (i) representative local catches of rare species require repeated sampling efforts (Martikainen and Kaila 2004), and (ii) rare species dependent on higher amounts of deadwood are difficult to model due to their low abundance in trap catches. Secondly, except for crown deadwood, the microhabitats were only measured on trunks and on live trees. The real density of cavities was probably underestimated, especially for oak with frequently-occurring cavities on large low branches within the tree crown. The density of lignicolous fungi, used as a proxy for fungal resources, was also undoubtedly underestimated since only large fruiting bodies were surveyed and one fungus at most was recorded per tree in the protocol. Moreover, the leaf cover may have hindered observations of microhabitats on the trunk; this could also have contributed to an underestimation of their number. The relationships between saproxylic and microhabitat diversity therefore require further investigations though such tree microhabitat surveys may be costly.

Perspectives

Perspectives for bio-indicator validation

Deadwood has become a centerpiece for forest monitoring in Europe. Since assessing stand structural elements is much faster and easier than inventorying species, deadwood is being

widely used to indicate the conservation value of forests (Noss 1999). More precisely, deadwood volume is considered to be an important indicator of forest biodiversity (Larsson 2001) and, as such, has been selected by the European Environmental Agency as an assessment criterion for sustainable forest management practices (EEA 2007). However, a validation of deadwood indicators at a wide geographical scale is still lacking (Stokland et al. 2004). Large downed deadwood volume was a significant predictor of beetle species richness in oak forests only. Deadwood diversity provided more consistent predictive models of the local number of saproxylic beetle species than volume variables in deciduous forests. In coniferous forests, deadwood diversity has also proven to be a better predictor of species richness than volume (pine: Brin et al. 2009, fir and spruce: Bouget, pers. com.). Using diversity variables can reduce the time spent sampling deadwood since presence/absence data from each type category is sufficient (Brin et al. 2009). Other studies have demonstrated that deadwood diversity is an efficient surrogate for many forest-dwelling species presence, including taxa that are not directly dependent on deadwood (e.g. Fritz et al. 2008). Finally, when we combined deadwood diversity and microhabitat diversity (i.e. the number of both deadwood and microhabitat types) in a single additive index, there was only a negligible increase in explanatory power on beetle species richness, compared with deadwood diversity alone (from $R^2 = 0.33$ to $R^2 = 0.34$ in all deciduous plots). The validation of ecologically-relevant indirect biodiversity indicators which are easy to survey based on data from national forest inventories, would require further large-scale and multi-taxonomic analyses. These features will also serve as criteria for more effective selection of conservation areas.

Implications for forestry

Substantial evidence exists that commercial forestry has a negative impact on deadwood quantity (Fridman and Walheim 2000). Several studies have reported that the diversity of deadwood substrates is also altered by forestry (e.g. Ekbom et al. 2006). We found that deadwood diversity is a consistent key factor for saproxylic beetle diversity; we therefore suggest that forest managers favor the local diversification of deadwood types rather than any given target volume (but see below in oak forests). From our analyses, deadwood positions and tree species were key dimensions for the effect of deadwood diversity on species richness; overall, the number of tree species was outstanding. In managed forests, forestry is known to induce (i) a depleted local diversity of tree species in deadwood, due to the counter-selection of many native tree species that are not considered economically valuable, and (ii) a decreased local diversity of deadwood positions, mainly due to the elimination of standing deadwood, perceived as a safety hazard (Bishop et al. 2009). It therefore seems relevant to increase the number of combinations of positions and tree species (except introduced exotic species) to favour the local species richness of saproxylic beetles. Moreover, further ecological studies should pay more attention to mixed coniferous–deciduous forests.

Our statistical breakpoints of deadwood or microhabitat values in the accumulation rate of species can not be translated into management targets as ecologically meaningful aggregation of true species extinction thresholds. It should however be borne in mind that threshold analyses did not consider the spatial structure of the data, despite the importance of site effects. Nonetheless, they may inspire cost-effective management guidelines. For instance, the efforts to retain just 1 fungus-bearing tree per ha would significantly increase beetle species richness and would be cost-effective. In our data, the strongest increase in rare species richness in beech forests and in common species in oak forests indeed occurred

from 0 to 1 fungus-bearing tree per ha. The rate of increase in species richness actually slightly slows down beyond the value of 1 tree per ha.In oak forests, an effort of downed deadwood restoration up to the target of 50 m^3 per ha would be efficient from an ecological perspective (though a bit costly in terms of forestry benefits), since the number of common species increased more slowly with deadwood volume beyond the value of 46 m^3 per ha. Nevertheless, it should be made clear that such quantitative deadwood targets would not meet the needs of all species; deadwood-dependent species are extremely numerous, and their deadwood requirements are species-specific (Müller and Bütler 2010). Finally, since stand openness strongly affected species composition, deadwood and microhabitats should be managed both under closed-canopy and open conditions (Vodka et al. 2009).

Perspectives for further approaches

One shortcoming of most of the empirical studies on saproxylic organisms is that they are typically conducted at a single, relatively small spatial scale. However, the probability of occurrence of saproxylic beetles is known to increase with the amount of dispersal sources in the surrounding landscape (e.g. Gibb et al. 2006). Moreover, habitat distribution may be more important than habitat quality in fragmented forest areas (Brunet and Isacsson 2009) like the temperate forests in Western Europe. One explanation for the lack of clear results on the relationship between deadwood or microhabitat density and biodiversity may be that resources have not been measured over an area large enough to reflect deterministic influences on local beetle assemblages, especially for aerially dispersing beetle species (Bishop et al. 2009). To date, only a few studies have shown the positive effects of deadwood volume on local saproxylic beetle species richness (Franc et al. 2007; Gibb et al. 2006; Økland et al. 1996) or deadwood-rich stands (Franc et al. 2007) in the surrounding landscape (from 100 m to 1 km). Considering the effects of regional deadwood on local assemblages might make a better spatial match between inventories and ecological processes (Turner and Tjørve 2005). Even if stand specific deadwood thresholds supply some information about the local richness and abundance of a species group, landscape-level deadwood thresholds would be necessary when considering the viability of meta-populations (Ranius and Fahrig 2006).

Local assemblages may also be considerably affected by delayed effects of past gaps in the continuity of the local deadwood supply, continuity which is critical for species long-term persistence (Jonsell and Nordlander 2002). Including more data about the history of deadwood availability would improve the explanatory power of assembly rules in saproxylic communities.

Acknowledgments We are grateful to Y. Paillet, A. Lassauce, C. Moliard (Irstea), T. Noblecourt, T. Barnouin, F. Soldati (ONF), N. Debaive (RNF), J. Willm, L. Burnel (INRA) and all the local forest managers for their field and laboratory work, and to F. Gosselin for helpful comments during the project, and Vicki Moore who checked the English language, and two anonymous reviewers whose detailed comments deeply improved our manuscript. This research was funded by the French Ministry in Charge of the Ecology through the BGF program (convention RESINE CVOJ000150, convention 10-MBGD-BGF-1-CVS-092, n°CHORUS 2100214651) and the National Forestry Board (ONF-Cemagref convention, Action 5, 2008). Part of this work was funded by the French Environment and Energy Management Agency (ADEME).

References

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84:511–525

Bishop DJ, Majka CG, Bondrup-Nielsen S, Peck SB (2009) Deadwood and saproxylic beetle diversity in naturally disturbed and managed spruce forests in Nova Scotia. Zookeys 22:309–340
Bouget C, Brustel H, Zagatti P, Noblecourt T (2010) The French information system on saproxylic beetle ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation statuts. http://frisbee.nogent.cemagref.fr/index.php/en/. Accessed 15 Jan 2013
Bouget C, Brin A, Brustel H (2011) Exploring the last biotic frontier: are temperate forest canopies special for saproxylic beetles? Forest Ecol Manag 261:211–220
Bouget C, Nusillard B, Pineau X, Ricou C (2012) Effect of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags. Insect Conserv Divers 5:264–278
Brin A, Brustel H, Jactel H (2009) Species variables or environmental variables as indicators of forest biodiversity: a case study using saproxylic beetles in maritime pine plantations. Ann Forest Sci 66:1–11
Brin A, Bouget C, Brustel H, Jactel H (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. J Insect Conserv 15:653–669
Brunet J, Isacsson G (2009) Influence of snag characteristics on saproxylic beetle assemblages in a south Swedish beech forest. J Insect Conserv 13:515–528
Burnham KP, Anderson DR (eds) (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, Berlin
Cobb TP, Hannam KD, Kishchuk BE, Langor DW, Quideau SA, Spence JR (2010) Wood-feeding beetles and soil nutrient cycling in burned forests: implications of post-fire salvage logging. Agric Forest Entomol 12(1):9–18
Dodelin B, André J, Wlérick L, Lempérière G (2004) Le bois mort en forêt de montagne (Alpes françaises). R. F. F. 66:507–518
EEA (2007) Halting the loss of biodiversity by 2010: proposal for a first set of indicators to monitor progress in Europe. Luxembourg: European Environment Agency, 186 p. ISBN 978-92-9167-931-7
Ekbom B, Schroeder LM, Larsson S (2006) Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. Forest Ecol Manag 221:2–12
Franc N, Gotmark F, Okland B, Norden B, Paltto H (2007) Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. Biol Conserv 135:86–98
Frank AF (2011) R-hacks/mer-utils.R. https://github.com/aufrank/R-hacks/blob/master/mer-utils.R. Accessed 15 Jan 2013
Fridman J, Walheim M (2000) Amount, structure and dynamics of deadwood on managed forestland in Sweden. Forest Ecol Manag 131:23–36
Fritz O, Gustafsson L, Larsson K (2008) Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biol Conserv 141:655–668
Gibb H, Hjältén J, Ball JP, Atlegrim O, Pettersson RB, Hilszczanski J, Johansson T, Danell K (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. Ecography 29:1–14
Grove SJ (2002a) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33:1–23
Grove SJ (2002b) Tree basal area and deadwood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecol Indic 1:171–188
Hothorn T, Hornik K, Zeilis A (2006) Party: a laboratory for recursive part(y)itioning (2006). http://CRAN.R-project.org/. Accessed 20 August 2012
Jonsell M, Nordlander G (2002) Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of deadwood. Forest Ecol Manag 157:101–118
Koch Widerberg M, Ranius T, Drobyshev I, Nilsson U, Lindbladh M (2012) Increased openness around retained oaks increases species richness of saproxylic beetles. Biodivers Conserv 21:3035–3059
Larjavaara M, Muller-Landau HC (2010) Comparison of decay classification, knife test and two penetrometers for estimating wood density of coarse woody debris. Can J Forest Res 40:2313–2321
Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Can J Forest Res 42:1433–1445
Larsson TB (Ed) (2001) Biodiversity evaluation tools for European forests. Ecol Bull 50:1–240
Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol Indic 11:1027–1039
Martikainen P, Kaila L (2004) Sampling saproxylic beetles: lessons from a 10 year monitoring study. Biol Conserv 120:171–181

Martikainen P, Siitonen J, Punttila P, Kaila L, Rauh J (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol Conserv 94:199–209
Müller J, Bütler R (2010) A review of habitat thresholds for deadwood: a baseline for management recommendations in European forests. Eur J Forest Res 129:981–992
Nilsson SG, Niklasson M, Hedin J, Aronsson G, Gutowski JM, Linder P, Ljungberg H, Mikusinski G, Ranius T (2002) Densities of large living and dead trees in old-growth temperate and boreal forests. Forest Ecol Manag 161:189–204
Noss RF (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. Forest Ecol Manag 115:135–146
Økland B, Bakke A, Hagvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers Conserv 5:75–100
Päivinen J, Ahlroth P, Kaitala V, Suhonen J (2003) Species richness and regional distribution of myrmecophilous beetles. Oecologia 134:587–595
Parmain G, Dufrene M, Brin A, Bouget C (in press) Influence of sampling effort on saproxylic beetle diversity assessment. Implications for biomonitoring studies in European temperate forests. Agric Forest Entomol 15:135–145
Ranius T (2002) Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol Conserv 103:85–91
Ranius T, Fahrig L (2006) Targets for maintenance of deadwood for biodiversity conservation based on extinction thresholds. Scand J Forest Res 21:201–208
Ranius T, Jansson N (2002) A comparison of three methods to survey saproxylic beetles in hollow oaks. Biodivers Conserv 11:1759–1771
Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms : Fennoscandian boreal forests as an example. Ecol Bull 49:11–41
Siitonen J, Martikainen P, Punttilä P, Rauh J (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecol Manag 128:211–225
Sippola A, Siitonen J, Kallio R (1998) Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish lapland. Scand J Forest Res 13:204–214
Stokland JN, Tomter SM, Söderberg GU (2004) Development of deadwood indicators for biodiversity monitoring: experiences from Scandinavia. In: Marchetti M (ed) Monitoring and indicators of forest biodiversity in Europe—from ideas to operationality. European Forest Institute, EFI proceedings n°51, pp 207–226
Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in deadwood. Cambridge University Press, Cambridge
Turner WR, Tjørve E (2005) Scale-dependence in species-area relationships. Ecography 28:721–730
Vodka S, Konvicka M, Cizek L (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. J Insect Conserv 13:553–562
Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecol Manag 255:1251–1261
Yoshimoto J, Kakutani T, Nishida T (2005) Influence of resource abundance on the structure of the insect community attracted to fermented tree sap. Ecol Res 20:405–414
Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

Article 7: Increasing the percentage of forest reserves in the landscape amplifies saproxylic beetle diversity both within and beyond reserve borders

Suite à des corrections, le titre de l'article a changé.

Effects of landscape design of forest reserves on Saproxylic beetle diversity. DOI: 10.1111/cobi.12572

APTARA | COBI | cobi12572 | Dispatch: August 11, 2015 | CE: AFL
Journal | MSP No. | No. of pages: 11 | PE: Michelle McCauley

Contributed Paper

Effects of landscape design of forest reserves on Saproxylic beetle diversity

C. Bouget* and G. Parmain*†‡ ¶

*National Research Institute of Science and Technology for Environment and Agriculture, Forest Ecosystems Research Unit, Domaine des Barres, F-45290, Nogent-sur-Vernisson, France
†National Laboratory of Forest Entomology, National Forest Office, F-11500, Quillan, France
‡National Museum of Natural History, Natural Patrimony Department, 36 rue Geoffroy St Hilaire, CP 41 75 231, Paris, CEDEX 05, France

Abstract: *Increasing the density of natural reserves in the forest landscape may provide conservation benefits for biodiversity within and beyond reserve borders. We used 2 French data sets on saproxylic beetle) and landscape cover of forest reserves (LCFR) to test this hypothesis: national standardized data derived from 252 assessment plots in managed and reserve stands in 9 lowland and 5 highland forests and data from the lowland Rambouillet forest, a forested landscape where a pioneer conservation policy led to creation of a dense network of reserves. Abundance of rare and common saproxylic species and total saproxylic species richness was higher in forest reserves than adjacent managed stands only in highland forests. In the lowland regional case study, as LCFR increased total species richness and common species abundance in reserves increased. In this case study, when there were two or more reserve patches, rare species abundance inside reserves was higher and common species richness in managed stands was higher than when there was a single large reserve. Spillover and habitat amount affected ecological processes underlying these landscape reserve effects. When LCFR positively affected species richness and abundance in reserves or managed stands, >12-20% reserve cover led to the highest species diversity and abundance. This result is consistent with the target of 17% forested land area in reserves set at the Nagoya biodiversity summit in 2010. Therefore, to preserve biodiversity we recommend at least doubling the current proportion of forest reserves in European forested landscapes.*

Keywords: Forest management, habitat amount, spillover effect, SLOSS, temperate

Efectos del Diseño de Paisaje de las Reservas de Bosques Sobre la Diversidad de Escarabajos Saproxílicos

Resumen: *El incremento de la densidad de reservas naturales en el paisaje boscoso puede proporcionar beneficios para la biodiversidad dentro y más allá de los límites de la reserva. Usamos dos conjuntos de datos franceses sobre los escarabajos saproxílicos y la cobertura de paisaje de las reservas de bosques (CPRB) para probar esta hipótesis: los datos estandarizados nacionales derivados de 252 planes de evaluación en puestos manejados y de reserva en nueve bosques de tierras bajas y en cinco de tierras altas y los datos del bosque de Rambouillet de tierras bajas, un paisaje boscoso en el cual una política pionera de conservación llevó a la creación de una densa red de reservas. Sólo en los bosques de tierras altas, la abundancia de especies saproxílicas raras y comunes y la riqueza total de especies saproxílicas fueron mayores en las reservas de bosques que en los puestos manejados adyacentes. En el estudio de caso regional de los bosques de tierras bajas, conforme incrementó la CPRB, incrementó la riqueza total de especies y la abundancia de especies comunes en las reservas. En este estudio de caso, cuando hubo dos o más parches de reserva, la abundancia de especies raras dentro de las reservas fue mayor y la riqueza de especies comunes en los puestos manejados fue más alta cuando hubo una sola reserva grande. El derrame y la cantidad de hábitat afectaron a los procesos ecológicos subyacentes a estos efectos de reserva de paisaje. Cuando la CPRB afectó positivamente a*

¶*Address correspondence to G. Parmain, email guilhem.parmain@irstea.fr*
Paper submitted December 11, 2014; revised manuscript accepted June 9, 2015.

DOI: 10.1111/cobi.12572

la riqueza y a la abundancia de especies en las reservas o en los puestos manejados, >12-20% de la cobertura de la reserva llevó a una diversidad y una abundancia de especies más alta. Este resultado es consistente con el objetivo fijado en la cumbre de 2010 en Nagoya de 17% de área de suelo boscoso en las reservas. Por esto, para preservar la biodiversidad, recomendamos por lo menos duplicar la proporción actual de reservas de bosque en los paisajes boscosos de Europa.

Palabras Clave: bosque templado, cantidad de hábitat, efecto de derrame, manejo de bosques, SLOSS, umbral

Introduction

Strategies to slow biodiversity loss include the setting up of networks of protected areas. For many years, biologists have discussed the optimal design of nature reserves (minimum size, distribution, density, total surface area) (Meffe & Carrol 1997). The amount of protected habitat in managed territories however remains restricted by human land use. Reserves would be more efficient if their conservation benefits extended into surrounding unprotected habitat. As a result of within-patch dynamics, reserves are thought to support an increased density of species, leading to a "spillover" (Gell & Roberts 2003) of these species into the surrounding stands. The density of reserves in the landscape may also affect species richness in the reserves themselves. The habitat-amount hypothesis predicts that species richness in equal-sized sample sites in reserve areas increases due to the total amount of reserve habitat in the surrounding landscape rather than increasing connectivity between reserve patches (Fahrig 2013). In addition to the question about reserve proportion effects at the landscape level on species biodiversity, the spatial organization of reserves is still debated. The same amount of reserve can be configured two ways: single large or several small reserve patches (Meffe & Carrol 1997). Both strategies seem useful, depending on the context (Tjørve 2010).

Most, if not all, European forests have been anthropogenically disturbed for several thousand years and have been affected by this disturbance in extent, structure, and composition (Parviainen et al. 2000). Current managed forests differ greatly from pristine forests. Forest preservation is rooted in the protection of forests for aesthetic reasons (e.g., preservation of the famous Fontainebleau forest in the middle of the 19th century) (Koop 1989). In France the first official and strict forest reserves for nature conservation were created in the 1950s, but many were established quite recently (Table 1). Nonetheless, some plots inside reserve areas have been unharvested for longer than others (although data on the last timber harvests are mostly unavailable). For instance, the Chene Brule and the Gros Fouteau reserves in the Fontainebleau forest were created in 1953 and 1970, respectively. Within these reserves, some core areas have not been harvested since 1861. General forest depletion due to worldwide forestry practices threatens deadwood-associated (i.e., saproxylic) species. Forest reserves harbor higher densities of old-growth structures, such as old trees and deadwood, that are favorable to saproxylic organisms than harvested forest matrix (Bouget et al. 2014).

In fine-grain managed forests in Western Europe, forest reserve patches) are often small and scattered in the landscape, which reduces local saproxylic population sizes and impedes their dispersal (Tscharntke et al. 2002). Benefits of reserves for biodiversity within and beyond reserve boundaries may be assessed by measuring biodiversity variations along two gradients of habitat isolation: distance to neighbouring reserves and density of reserves in the surrounding landscape. There is a significant positive effect of neighbouring old-growth stands on biodiversity in terms of surrounding reserve density (Gibb et al. 2006; Franc et al. 2007; Abrahamsson et al. 2009; Olsson et al. 2012) and in terms of linear distance (McGeoch et al. 2007; Brunet and Isacsson 2009; Rotheray et al. 2014). We used the proportion of reserves within a forest landscape, hereafter called landscape cover of forest reserves (LCFR), as a predictive variable rather than distance to the nearest neighbouring habitat patch (following Moilanen & Nieminen 2002). The fact that Fahrig (2013) questioned whether connectivity beyond habitat amount has an effect in terrestrial ecosystems also supports our choice of LCFR instead of connectivity measures. We hypothesized that species richness or abundance in harvested areas is greater when LCFR is relatively higher in the surrounding landscape. Highland forests are more difficult and expensive to harvest than lowland forests and have a high quantity of deadwood (Seibold et al. 2015) relative to lowland forests, where the difference between reserves and harvested stands is sharper. As a consequence, we expected less of an effect of LCFR on species richness or abundance in managed areas surrounding highland than lowland reserves. Similarly, effects of habitat amount may be stronger in lowland than in highland forests.

We analyzed saproxylic beetle data from 14 French temperate forests to address the following five questions: In accordance with our hypothesis, is reserve cover in the surrounding forest landscape a significant factor in predicting variations in local species richness on harvested plots? In compliance with the habitat amount hypothesis, does reserve cover in the surrounding landscape significantly affect local species richness in the reserves themselves? Are both effects lower in highland forests? Are

Table 1. Study plot and insect trap (for saproxylic beetles) distribution.

Elevation	*Forest name*	*Forest composition*	*Project (year)*	*Plot type*	*No. plots (no. of traps)*	*Deadwood volume per plot (m^3/ha)*			*Elevation range (m)*	*Reserve creation date*
						mean	*max*	*min*		
Highland	Ballons-Comtois	fir-beech	GNB[a] (2010)	MAN[b]	8 (16)	49.85	117.24	20.29	980-1080	1984
				RES[c]	8 (15)	69.87	154.37	28.31		
	Engins	spruce	GNB (2011)	MAN	5 (10)	26.01	35.69	8.99	1510-1640	2010
				RES	4 (8)	27.06	65.38	3.83		
	Lure	fir-beech	GNB (2011)	MAN	4 (8)	23.32	54.56	5.66	1340-1600	2013?
				RES	4 (8)	67.62	182.42	11.83		
	Ventoux	fir-beech	GNB (2011)	MAN	5 (10)	20.49	33.55	11.54	1260-1500	2010
				RES	5 (10)	114.99	191.88	34.72		
	Ventron	fir-beech	GNB (2009)	MAN	4 (8)	46.94	93.26	13.4	810-1040	1989
				RES	4 (8)	46.46	88.02	16.36		
Total highland				MAN	26 (52)					
				RES	25 (49)					
Lowland	Auberive	beech	GNB (2009)	MAN	12 (24)	19.08	51.69	1.78	320-450	1993
				RES	12 (24)	59.04	161	0.85		
	Bois_du_Parc	oak-hornbeam	GNB (2011)	MAN	5 (5)	3.7	13.06	0.51	150-210	1979
				RES	5 (5)	10.44	23.47	3.67		
	Chizé	oak-beech	GNB (2010)	MAN	12 (24)	13.54	29.31	4.77	60-100	2006
				RES	12 (24)	23.44	96.78	0.51		
	Citeaux	oak-beech	GNB (2010)	MAN	6 (12)	14.57	35.45	3.02	190-200	1989
				RES	6 (12)	70.37	111.76	8.12		
	Combe-Lavaux	oak-beech	GNB (2010)	MAN	4 (8)	8.9	20.49	1.03	300-500	2004
				RES	4 (8)	18.64	60.48	1.01		
	Fontainebleau	oak-beech	GNB (2008)	MAN	13 (25)	18.08	46.05	2.56	60-140	1953-1996
				RES	12 (24)	175.56	371.16	32.27		
	Haut-Tuileau	oak-hornbeam	GNB (2011)	MAN	7 (7)	18.72	61.3	5.33	160-170	2008
				RES	7 (7)	13.39	22.15	1.75		
	Rambouillet	oak-hornbeam	GNB (2012)	MAN	8 (16)	11.46	27.36	1.18	140-150	1993-2007
				RES	8 (16)	17.93	45.22	0.51		
	Rambouillet	oak-hornbeam	RESINE (2006-07)	MAN	44 (88)	41.31	111.28	1.4	130-160	1993-2007
				RES	16 (32)	65.03	138.36	2.88		
	Verrières	oak-hornbeam	GNB (2012)	MAN	4 (8)	26.55	47.64	2.65	160-170	2004
				RES	4 (8)	84.91	159.68	11.73		
Total lowland				MAN	115 (217)					
				RES	86 (160)					
Total				MAN	141 (269)					

[a]*Gestion, Naturalité et Biodiversité, French program studying reserve effects on saproxylic biodiversity.*
[b]*Managed plots.*
[c]*Reserves plots.*

Table 2. Summary of spatial scale models of the effects of forest reserve area on richness of common beetle species and on richness and abundance of rare beetle species.[a].

			Lowland		*Highland*	
Data set			*MAN*	*RES*	*MAN*	*RES*
National data set (y~a+b) [b]	forest reserve surface	SRtot[d]	ns	ns	2500 m (+[c])*	ns
		SRcom	ns	ns	Ns	ns
		Abcom	T[c,d] 2500 m (-[d])**	ns	2500 m (+)***	ns
		SRrar	Ns	ns	ns	ns
		Abrar	Ns	ns	T 2500 m (+)*	ns
Regional case study (y~a+b+c)	forest reserve surface	SRtot	Ns	T 2500 m (+)**	NA	NA
		SRcom	Ns	ns	NA	NA
		Abcom	Ns	T 2500 m (+)**	NA	NA
		SRrar	Ns	ns	NA	NA
		Abrar	Ns	ns	NA	NA
		SRtot	T 2500 m (+)*	ns	NA	NA
		SRcom	Ns	ns	NA	NA
	Nb patches	Abcom	Ns	ns	NA	NA
		SRrar	Ns	ns	NA	NA
		Abrar	Ns	2500 m (+)*	NA	NA

[a] *The significance of the models is indicated after the best spatial scale effect (*p = 0.05;**p = 0.001; ***p<0.001. Abbreviations: MAN, managed plots; RES, reserve; T, detection of a threshold; SRcom, richness of common species; SRrar, richness of rare species; Abrar, abundance of rare species; SRtot, total species richness y = c(SRcom or SRrar or Abrar);*

[b] *y = c(SRcom or SRrar or Abrar). Variables: a, deadwood volume; b, forest reserve surface area; c, number of patches.*

[c] *Positive effect of b or c on y.*

[d] *Negative effect of b or c on y.*

common or only rare species affected by reserve cover in the surrounding landscape (i.e., are rare species possibly more sensitive to the distribution pattern of reserves)? Does the number of reserve patches affect local species richness after accounting for the effects of reserve cover (in the lowland regional case study only)?

Methods

Study Sites

We set up 252 plots (111 plots in forest reserves and 141 in managed stands) in mature forest stands (at least 100 years old), dominated by spruce, fir, beech, or oak, in 14 French forests (9 lowland and 5 highland forests) (Table 1). All study forests included managed and reserve plots. Among our study sites, the Rambouillet forest is a special case. Certain conservation measures were pioneered in this 22,000-ha state oak forest in northern France, 50 km west of Paris. The forest currently includes a functional network of forest reserves that have remained unharvested for more than 80 years. The Rambouillet forest was studied by the GNB (2012) and RESINE (2006-2007) projects; the latter had a denser sampling design.

Beetle Data

Flying saproxylic beetles were sampled with two unbaited cross-vane flight interception traps (PolytrapTM, E.I. Purpan, Toulouse, France) per plot. Traps were suspended roughly 1.5 m above the ground and set about 20 m apart, except for the Bois du Parc and Haut-Tuileau sites, where only one trap per plot was set. A total of 478 traps were set. Active insects were collected from April to August (see Table 1 for sampling years). In the approximately 50 recorded families, we distinguished rare and common species in France according to the FRISBEE database (http://frisbee.nogent.cemagref.fr/index.php/en/). We based commonness and rarity on geographic range and local abundance (Rabinowitz 1981). Rare species had a narrow range and abundance that was somewhere large or had a wide range and abundance that was small everywhere. Common species had a wide range and abundance that was somewhere large. The resolution of species identification was higher for the detailed regional data set than for the 14 other standardized data sets. In the standardized low-resolution beetle data set, we considered only the families systematically identified at all sites. We had a more specific objective (see below) with the high-resolution regional data set and analyzed it separately. We examined 5 response variables for each trap: total raw species richness (SRtot), common and rare raw species richness and abundance (SRcom, Abcom, SRrar, and Abrar respectively). Species richness was not standardized using abundance values.

Landscape and Environmental Data

While studying landscape effects on oak saproxylic beetles from the local to the large scale, Bergman et al. (2012)

found the 2300-m scale to be outstanding. We used a geographic information system (ArcGIS version 10.2) to quantify the proportion of forest area set aside as forest reserves within 2500 m of each plot (buffer zones). To avoid an artificial increase in LCFR values due to non-forest areas in the surrounding landscape, no plots were set near an external forest edge. In all our other study sites, only 1 or 2 reserves patches were available. In contrast, for the Rambouillet forest, over 10 reserve patches were available, which allowed us to analyze the number of reserve patches.

We computed the number of forest reserve patches inside each buffer in only the regional case study. We used deadwood volumes for each plot published in Bouget et al. (2014).

Data Analyses

Two data sets were available for analysis: a nationally compiled, standardized data set with lower taxonomic resolution for beetles but a larger overall sample size, broader landscape coverage, including both lowland and highland forests, and more regional replicates and a detailed regional case study of the single lowland Rambouillet forest, which offered high-resolution beetle data and had more, though more locally specific, reserves in the forest mosaic landscape (fewer replicates).

With the national data set, we performed separate analyses for lowland and mountain sites due to differences in the mean specific richness per trap and potential divergences in average management history. To account for between-trap differences due to local within-plot contrasts in resource availability, we included the local deadwood volume as a primary covariate in the analytical models. Depending on the distribution pattern of response variables, we used linear (lmer) or generalized linear (glmer, family = Poisson) mixed models. Forest was a random factor in all mixed models. An observation-level random effect was added in the generalized linear mixed models to account for data overdispersion. The effects of LCFR on beetle response variables were assessed at the 2500-m scale in harvested and in reserve stands with a likelihood ratio test between the models with and without the predictor.

In the regional case study, we used glmer models with LCFR and the number of reserve patches as additive effects and deadwood volume as a primary covariate. The number of reserve patches and LCFR were not significantly correlated (Pearson $r = 0.06$). We used likelihood ratio tests to assess the significance of ecological effects between models.

We used recursive partitioning (Hothorn & Zeileis 2008) to search for thresholds in LCFR in the significant models. One or more critical thresholds are derived from estimates of breakpoints revealed in maximally selected two-sample statistics. The validity of the thresholds was assessed with multiple tests. Based on 1000 bootstrap samples, a confidence interval (95% CI) was calculated for all thresholds. Significance for thresholds was set at $p<0.01$. Each of the 2 subsets separated by a threshold analysis had to contain at least 8 samples for the threshold result to be kept.

All analyses were carried out with R (version 3.1.0) (R Core Team 2013) software.

Results

The compiled standardized data set included 460 species and 179,237 individuals (Supporting Information), and the detailed regional data set had 335 species and 137,154 individuals. On average, the deadwood volume per plot was 2.7 higher in reserves than in harvested plots (Table 1). In agreement with our hypothesis, the contrast in deadwood volume between reserve and harvested areas was lower in highland (2.3 times) than in lowland (2.9 times) forests. In reserve and in harvested plots, average deadwood volumes were higher in highland (66.4 m^3/ha and 35.2 m^3/ha, respectively) than in lowland forests (51.6 m^3/ha and 17.8 m^3/ha, respectively).

Response of Beetle Assemblage to LCFR

In managed highland stands, the total species richness increased as LCFR increased; no threshold could be identified for this slightly significant relationship (Fig. 1a). The LCFR also contributed significantly to local variations in rare species and common species abundances (Fig. 1b and 1c). The abundance of rare species was positively affected by an increasing LCFR, and the forest reserve threshold value was 11.8% (CI 2.7-13.7) within the 2500-m buffer (Fig. 1b). The slope of the individual accumulation rate was steeper beyond the detected threshold point. This pattern was observed for all thresholds we detected.

In lowland managed stands at the national level, neither total species richness nor rare species abundance and richness significantly responded to variations in LCFR. The increasing LCFR however had a significant negative effect on common species abundance in lowland harvested stands. Similarly, in lowland harvested stands of the regional case study, the relationships between beetle assemblage metrics and LCFR were not significant. However, after taking LCFR into account, an increase in the number of reserve patches positively affected the total number of species in managed stands within the 2500-m buffer. The total species richness was amplified beyond the threshold value of two reserve patches in the 2500-m buffer (CI 1–3; Fig. 1d).

No response of total species richness to variations in LCFR was observed in highland reserves. Moreover,

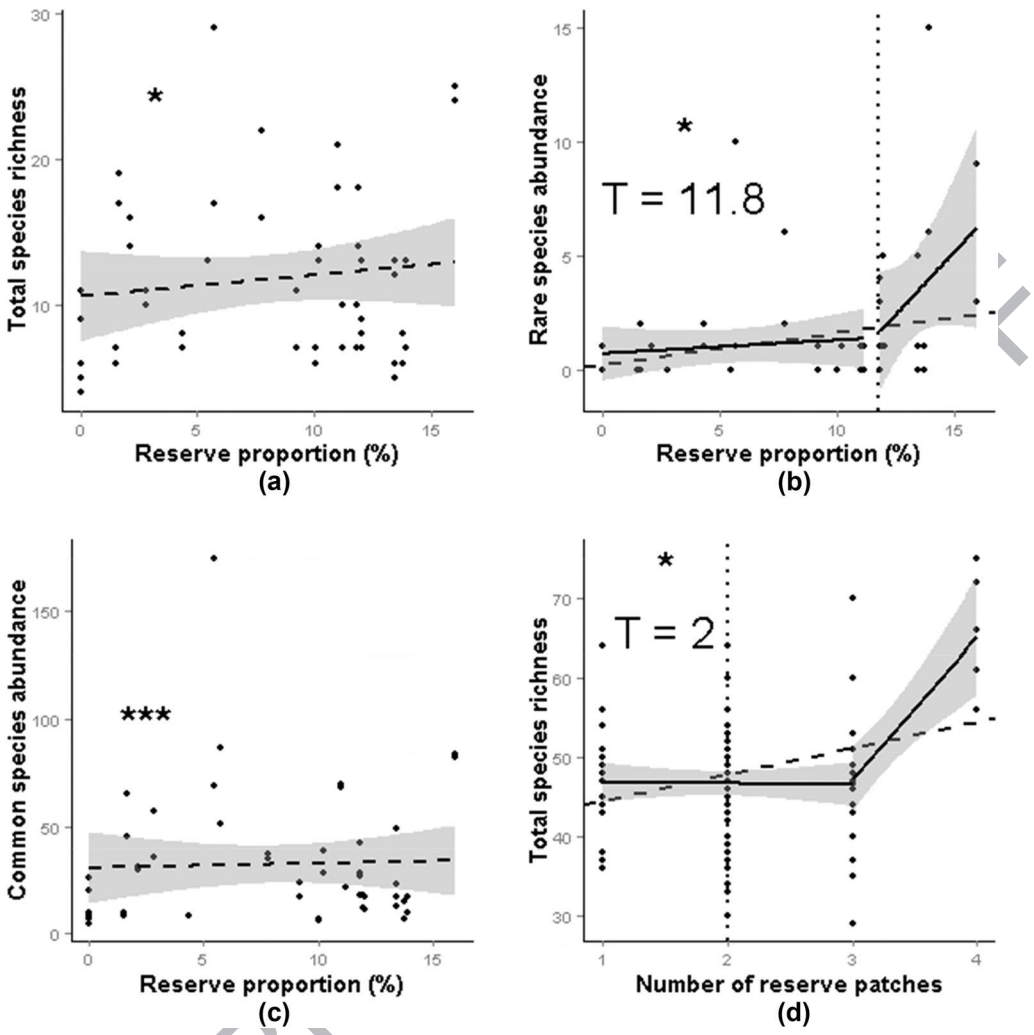


Figure 1. Response of beetle diversity and abundance in harvested forest plots to (a-c) the proportion of reserve forest in the landscape and to (d) the number of reserve patches in the surrounding landscape (2500 m scale) ([a-c], highland forests; [d], lowland regional case study (covered by axis labels); abundance, mean values per trap; dashed lines, linear species accumulation rate; vertical dashed lines threshold [T] of proportion of reserve forest or number of reserve patches after which the species accumulation rate significantly changes; continuous lines, species accumulation rate before and after threshold; ∗ $p = 0.05$; ∗∗∗$p = 0.001$; shaded areas, SD of accumulation rate curves, which are represented on global species accumulation rate when there is no threshold and on species accumulation rate before and after threshold lines when there is a threshold.

neither rare nor common species in reserve plots were affected in abundance or richness by variations in LCFR.

The saproxylic beetle species response to LCFR in lowland reserves differed from the response in highland reserves. Variations in LCFR did not significantly affect saproxylic beetle biodiversity in lowland reserves at the national scale. In contrast, in the regional case study, an increase in LCFR enhanced the total species richness and the abundance of common species in reserves in the 2500-m buffer . Both effects were even stronger beyond a threshold value of 20.0% (CI 20.0-20.9 for SRtot and 20.0-20.1 for Abcom) of LCFR (Fig. 2a and 2b). The number of reserve patches in the 2500-m buffer also significantly affected the abundance of rare species, although no threshold value was detected in this relationship (Fig. 2c). The number of surrounding reserve patches had no significant effect on total, common, or rare species richness in reserve plots.

Discussion

Potential Spillover Effect

Even though our sampling scheme was not experimentally designed to test for spillover effects, we did find that landscape reserve design benefitted biodiversity

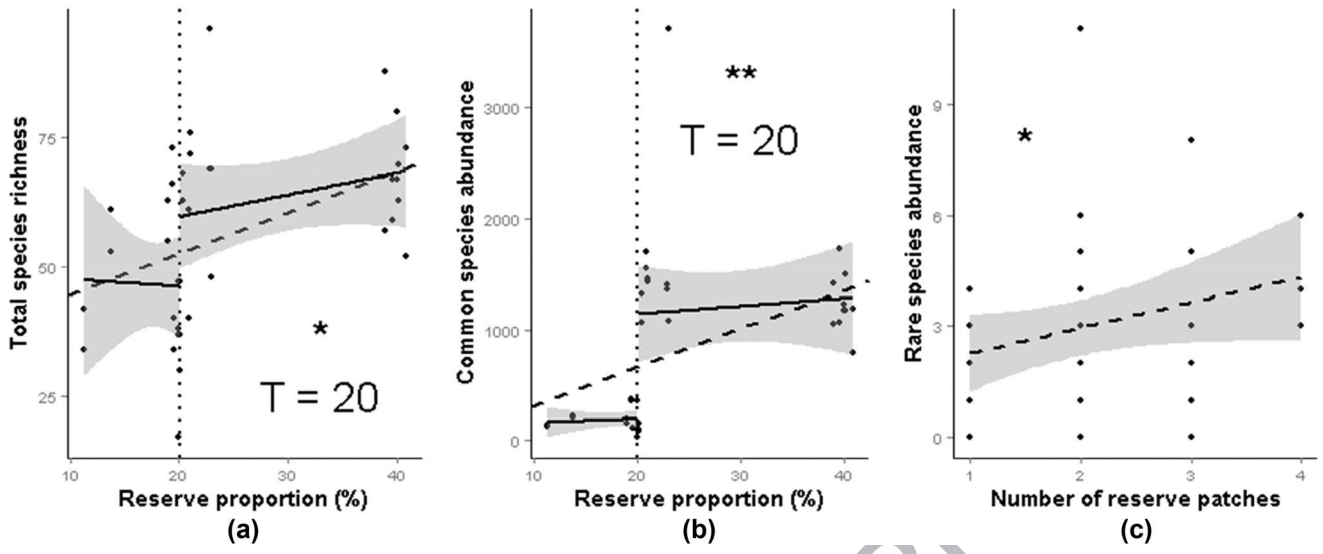


Figure 2. Response of beetle diversity in reserve plots (habitat amount hypothesis) to (a,b) the reserve proportion and the (c) number of reserve patches in the surrounding forest landscape (2500 m scale) in the lowland Rambouillet forest case study ([a], total species richness; [b], abundance of common species; [c], abundance of rare species; dashed lines, linear species accumulation rate; vertical dashed lines threshold [T] of proportion of reserve forest or number of reserve patches after which the species accumulation rate significantly changes; continuous lines, species accumulation rate before and after threshold; $*p = 0.05$; $**p = 0.01$; shaded areas, SD of accumulation rate curves, which are represented on global species accumulation rate when there is no threshold and on species accumulation rate before and after threshold lines when there is a threshold).

beyond reserve borders. These results may be related to the higher ecological quality of the reserves relative to the harvested areas. On average, the deadwood volume per plot was far higher in reserves than in harvested plots.

The spillover effect is conceptually close to the spatial mass effect (Shmida & Ellner 1984), which is based on the assumption that a species can occur in low-quality habitat, despite low reproductive success and fitness, thanks to the influx of propagules from a source population living in a nearby habitat of higher quality (Shmida & Ellner 1984). Due to its heuristic value in conservation ecology, the model has been extended from single species to species communities: spillover should cause species enrichment around reserves that host large numbers of species. Spillover effects were initially studied in marine ecosystems (McClanahan & Kaunda-Arara 1995) and have only recently been documented for insects in terrestrial ecosystems, from natural habitats to crop plantations (Lucey & Hill 2012) and from early to late mass-flowering crops (Riedinger et al. 2014). Reserve areas, thanks to their higher-quality habitat (Bouget et al. 2014) and larger populations, (edit may have changed meaning, but original was unclear) may be converted into nurseries for saproxylic beetle species, which may enable more dispersers to emigrate to nearby harvested stands. Landscape effects on the survival probability of individual species - and consequently on the local number of species persisting in matrix habitats - may be related to metapopulation processes, with recolonizing events counterbalancing local extinctions in fragmented landscapes (Hanski & Gagiotti 2004). Having more reserves inside a landscape buffer also improves connectivity and facilitates exchanges of individuals and species among reserve patches, thereby causing a connectivity-enhanced spillover effect. From Ranius et al. (2011), conservation efforts (e.g., restoration of favourable substrates for saproxylic target species) should focus on sites where colonisation is more likely.

The importance of the surrounding landscape for local species richness, here attested to in highly fragmented temperate forests in Western Europe, is in line with suggestions by Lassauce et al. (2011) and Bouget et al. (2013), who both demonstrated that local saproxylic biodiversity is not strongly driven by the quantity of locally available deadwood substrates. Even in boreal contexts, the structural and compositional habitat heterogeneity at the landscape scale contributes to a large degree to beetle richness patterns (Janssen et al. 2009).

Our hypothesis assuming a stronger spillover effect in lowland forests was proven invalid. Contrary to our expectations, the significant effect of LCFR on species richness or abundance in managed areas surrounding reserves was actually observed only in highland forests. However, in line with our hypothesis, average differences in deadwood volume between reserve and harvested areas were lower in highland than in lowland forests. Findings from a companion study also demonstrated fewer

differences between reserves and harvested stands relative to old-growth conditions (e.g., number of large live trees) in highland than in lowland beech forests (Pernot et al. 2013). Due to overall topographical constraints, forestry is generally more extensive in highland than in lowland forests. Less frequent harvests and continuous forest cover, associated with uneven-aged forestry in highland forests, is likely to only slightly affect the density of old-growth structures in managed areas relative to intensive lowland management (Lafond et al. 2014). Throughout our sampling design, highland forests also had a large quantity of deadwood substrates in harvested areas (see also Seibold et al. 2015). Both in reserves and in harvested plots, average deadwood volumes were higher in highland than in lowland forests. The better past habitat continuity in highland than in lowland reserves, or in the regional case study than in other lowland sites, could strengthen their current spillover effect. An enhanced spillover effect from highland forest reserves is also in line with another finding. We demonstrated that the deadwood-biodiversity relationship is stronger under colder conditions (Lassauce et al. 2011, Müller et al. 2015). Among lowland sites, the regional case study is special because reserves there have been established mainly based on their conservation value (i.e., on sites with high substrate continuity in the past). No historical data are available to support this point.

Also contrary to one of our hypotheses, significant effects of increasing LCFR were observed on rare but also on common species (in abundance). From our results in managed highland temperate forests, reserves acted as source areas for both common and rare saproxylic species. Hjältén et al. (2012) underlined the importance of reserves for maintaining viable populations of rare red-listed species in boreal forest landscapes.

Not all saproxylic beetle species favoured habitat conditions in forest reserve patches. Some substrates, such as fresh deadwood, are promoted by forestry and are less available in landscapes where the reserve cover is high. In lowland forests at the national level, increases in LCFR led to decreases in common species abundance in harvested stands. We observed that bark beetles associated with fresh deadwood were mainly responsible for peaks of common species abundance in landscapes with a low reserve cover.

Habitat Amount Effect

The increasing LCFR in the 2500-m buffer did not affect biodiversity in the reserves in the national lowland or highland datasets, but it significantly increased (?) common species abundance and total species richness in the lowland regional case study. This positive influence on biodiversity in reserves of increasing reserves in the surrounding landscape is in line with the habitat amount hypothesis (Fahrig 2013). Contrary to expectations, this habitat amount effect on biodiversity in reserves was not stronger in lowland than in highland forests or stronger for rare than for common species. But in agreement with our hypothesis, only rare species (in abundance) were positively and significantly affected by the number of patches in the regional case study.

Response Thresholds to the Proportion of Reserves

Habitat thresholds may help managers define targets for conservation (Müller & Bütler 2010). We identified and showed the importance of non-linear relationships between landscape patterns and beetle assemblage metrics. We included the reserve-and-managed paired configuration of our sampling design in our modeling approach (with a "forest" random effect) but did not account for detailed spatial autocorrelation between plots inside each forest. All detected values were low thresholds (i.e., minimum values beyond which benefits for biodiversity conservation strongly increased). In all cases, the species or individual accumulation rate strongly increased beyond the threshold value. These thresholds correspond to the amount of habitat below which fragmentation may affect population persistence (Andrén 1994). Threshold values could be more accurately defined with larger data sets. Larger dedicated data sets would make the range of studied LCFR values more continuous. The LCFR values between 25% and 40% were not available in the 2500-m buffer in the lowland regional case study. The significant threshold values we detected were higher than 10% of habitat. These threshold effects were demonstrated for beetle assemblage metrics in reserves and harvested plots. The abundance of rare species in highland harvested areas increased greatly beyond 12% LCFR. Total species richness and abundance of common taxa in reserves increased beyond 20% LCFR in the lowland regional case study. Gustafsson et al. (2012) suggest that amount of favorable habitat within a production forest should be above 5–10% to achieve an ecological enrichment. Several authors advocate conserving 20–30% of high-quality habitat for biodiversity conservation at the landscape scale (Andrén 1994, Nilsson et al. 2001, Wiktander et al. 2001). Because extinction thresholds differ widely among species (Holland et al. 2005), distinct thresholds in habitat availability at the species assemblage level would be difficult to determine (Ranius & Fahrig 2006). From our results, but contrary to the hypothesis, threshold values were lower for rare than for common species. High values of landscape reserve cover are likely to encompass most saproxylic species' habitats.

The threshold values we detected among landscape-biodiversity relationships, from 12% to 20% of reserve cover in the landscape within the 2500-m buffer, are consistent with the target of reserving 17% of forested land area for conservation purposes, set at the UN biodiversity summit in Nagoya in 2010 (Hanski 2011). Such a

target is nonetheless ambitious compared with the current proportion of forest reserves across Europe: 7.6% on average (Parviainen et al. 2000) and ranging from 1.2% of the total forest cover in France to 24.0% in Spain. Only Spain, Denmark, and Hungary have a proportion of protected forests that slightly exceeds 20%. From 2000 to 2011, public forest surface area increased from 1.2% to 6.7% (ONF 2011). Fortunately, a large proportion of private forests in France, with their fragmented ownership, has been left unmanaged and unharvested; these patches act as unofficial passive reserves. From Bücking (2003), recommendations should be made not only on threshold area (reserve cover percentage) but also on threshold size and threshold numbers to optimise European protected forest networks.

Reserve Design and SLOSS

Our results from the lowland regional case study provide important information about the spatial design of reserves, a recurrent issue in biodiversity conservation (Lindenmayer et al. 2015). Within the 2500-m buffer, several small reserves more efficiently increased beetle species richness outside the reserves than did a single large reserve. This effect was amplified beyond the threshold value of two reserve patches. In the reserves themselves, an increasing number of patches in the surrounding landscape improved rare species abundance.

In the SLOSS debate (single large or several small), many authors conclude that large reserves generally are better for biodiversity conservation than small reserves (Meffe & Carrol 1997). Nevertheless Schwartz (1999) and Götmark and Thorell (2003) emphasize the value of small reserves (higher quality remnants, more connected), especially in highly fragmented landscapes that are strongly dominated by anthropic uses (agriculture, forestry, urbanization), where large connected reserves are difficult to establish. The lifeboating function of reserves is improved by small and more numerous reserves, whereas habitat quality is relatively high where there are a few large reserves that are relatively less affected by edge (Lindenmayer et al. 2015). Results of field studies differ, underlining the need for individual case studies to determine the best local strategy (Tjørve 2010). Metapopulation models from Ranius and Kindvall (2006) show that a few large forest reserves are more efficient than many small reserves in unharvested forests, but many small forest reserves are more efficient than several large reserves in harvested forests. Some studies offer guidelines for the minimum size of unharvested patches required to host a maximum diversity of substrates, for example, at least 20 ha for tree microhabitats (Larrieu et al. 2014) and at least 2 ha for deadwood types (Jakoby et al. 2010). In line with our findings, Ovaskainen (2002) suggest several large forest reserve patches in the landscape are more valuable for strengthening forest species metapopulations (e.g., saproxylic beetle populations, than one single reserve patch).

It should be borne in mind that criteria such as patch shape, edge length and contrast, connectivity, and corridors also determine reserve conservation value and that selection criteria in any forest conservation strategy should consider not only conservation value but also management costs. Large ecological reserves may be easier to protect from an organizational perspective. Conversely, single, large ecological reserve units are rarely comprehensive in terms of habitats, nor are they representative of all elements of biodiversity. Forest managers may therefore be better off protecting a wider range of habitats through smaller reserve patches distributed throughout the fine-scale mosaic of European land-cover types, or at least to adopt multi-scaled conservation measures.

We limited our investigation to the entire assemblage and groups of common and rare species. It should however be kept in mind that not all species depend on reserve patterns equally (Tscharntke et al. 2002). We therefore suggest that reserve patches could also provide interesting study areas for population dynamics of generalist and specialist species, species that disperse widely or occupy small home ranges, and single species. Further studies could also focus on the effects of reserve design on between-reserve or reserve-matrix complementarity in terms of species composition (Müller & Gossner, 2010) and on gamma diversity on at a regional scale.

Our results, which are based on a selection data from highland and lowland French forest, do not provide universal precepts. It should also be kept in mind that we observed forest context-dependent responses. Further research is therefore required to define relevant management guidelines for reserve design in order to increase levels of biodiversity spillover, in particular in relation to patch connectivity and patch shape. Establishing reserves in high-quality habitat patches is of primary concern. The present-day habitat quality in forest reserves is affected largely by local management history. Some reserves, unharvested over the last 50 years, were heavily harvested for centuries. Past management intensity may have long-term effects on saproxylic community composition. The colonization by saproxylic beetles is a very slow process that requires an even longer time frame than habitat restoration (Bouget et al. 2014). Benefits of recent but permanent reserves could tend to be tangible only in the long term (Gustafsson et al. 2012).

Acknowledgments

We are grateful to C. Moliard, B. Nusillard, Y. Paillet, F. Gosselin (Irstea), T. Barnouin, F. Soldati, T. Noblecourt (ONF), N. Debaive (RNF), J.L. Témoin, M. Bonafonte (ONF Rambouillet), and all the local forest managers for

their field and laboratory work and assistance. We are also indebted to V. Moore who reviewed the English manuscript. Helpful and constructive comments from the editor and 2 anonymous reviewers greatly improved an earlier version of the manuscript. This research was funded by the French ministry in charge of the Ecology through the Biodiversité, Gestion Forestière et Politiques Publiques (BGF) program (RESINE CVOJ 000 150 convention, 10-MBGD-BGF-1-CVS-092 convention, n°CHORUS 2100 214 651) and the National Forestry Board (Office National des Forets, ONF-Cemagref convention, Action 5, 2008).

Supporting Information

A list of collected species (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Abrahamsson, M., M. Jonsell, M. Niklasson, and M. Lindblahd. 2009. Saproxylic beetle assemblages in artificially created high-stumps of spruce (*Picea abies*) and birch (*Betula pendula/pubescens*)—does the surrounding landscape matter? Insect Conservation and Diversity **2:**284–294.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71:**355–366.

Bergman, K.O., N. Jansson, K. Claesson, M.W.Palmer, and P. Milberg. 2012. How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. Forest Ecology and Management **265:**133–141.

Bouget, C., G. Parmain, O. Gilg, T. Noblecourt, B. Nusillard, Y. Paillet, C. Pernot, L. Larrieu, and F. Gosselin. 2014. Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? Animal Conservation **17:**342–353.

Bouget, C., L. Larrieu, G. Parmain, and B. Nusillard. 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodiversity and Conservation **22:**2111–2130.

Brunet, J. and G. Isacsson. 2009. Restoration of beech forest for saproxylic beetles-effects of habitat fragmentation and substrate density on species diversity and distribution. Biodiversity and Conservation **18**, 2387–2404.

Bücking, W. 2003. Are there threshold numbers for protected forests? Journal of Environmental Management **67:**37–45.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography **40:**1649–1663.

Franc, N., F. Gotmark, B. Okland, B. Norden, and H. Paltto. 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. Biological Conservation **135:**86–98.

Gell, F.R., and C.M. Roberts. 2003. Benefits beyond boundaries: The fishery effect of marine reserves. Trends in Ecology and Evolution **18:**448–455.

Gibb, H., J. Hjältén, J. Ball, O. Atlegrim, R. Pettersson, J. Hilszczanski, T. Johansson, and K. Danell. 2006. Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. Ecography **29**: 1–14.

Götmark, F. and M. Thorell. 2003. Size of nature reserves: Densities of large trees and dead wood indicate high value of small conservation forests in southern Sweden. Biodiversity and Conservation **12**: 1271–1285

Gustafsson, L., et al. 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience **62:**633–645.

Hanski, I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio **40:**248–255.

Hanski, I., and O. E. Gagiotti. (Eds) 2004. Genetics and evolution of metapopulations. Academic Press.

Hjältén, J., F. Stenbacka, R.B. Pettersson, H. Gibb, T. Johansson, K. Danell, J.P. Ball, and J. Hilszczański. 2012. Micro and macro-habitat associations in saproxylic beetles: Implications for biodiversity management. PLoS ONE **7:**e41100. DOI: XXXX.

Holland, J.D., L. Fahrig, and N. Cappuccino.2005. Body size affects the spatial scale of habitat/beetle interactions. Oikos **110:**101–108.

Hothorn, T., and A. Zeileis. 2008. Generalized maximally selected statistics. Biometrics **64:**1263–1269.

Jakoby, O., C. Redemacher, and V. Grimm. 2010. Modelling deadwood islands in European beech forests: how much and how reliably would they provide deadwood? European Journal of Forest Research **129:**659–668.

Janssen, P., D. Fortin, and C. Hébert. 2009. Beetle diversity in a matrix of old-growth boreal forest: Influence of habitat heterogeneity at multiple scales. Ecography **32:**423–432.

Koop, H., 1989. Forest dynamics. Silvi Star: a comprehensive monitoring system. Springer, Berlin.

Lafond, V., G. Lagarrigues, T. Cordonnier, and B. Courbaud. 2014. Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity. Annals of Forest Science **71:**173–186.

Larrieu, L., A. Cabanettes, A. Brin, C. Bouget, and M. Deconchat. 2014. Tree microhabitats at the stand scale in montane beech-fir forests: practical information for taxa conservation in forestry. European Journal of Forest Research **133:**355–367.

Lassauce, A., Y. Paillet, H. Jactel, and C. Bouget. 2011. Deadwood as a surrogate for forest biodiversity: Meta analyses of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators **11:**1027–1039.

Lindenmayer, D.B., et al. 2015. Contemplating the future: Acting now on long-term monitoring to answer 2050's questions. Austral Ecology DOI: 10.1111/aec.12207.

Lucey, J.M., and J.K. Hill. 2012. Spillover of Insects from Rain Forest into Adjacent Oil Palm Plantations. Biotropica **44:**368–377.

McClanahan, T.R., and B. Kaunda-Arara. 1995. Fishery Recovery in a Coral-reef Marine Park and Its Effect on the Adjacent Fishery. Conservation Biology **10:**1187–1199.

McGeoch, M., M. Schroeder, B. Ekbom, and S. Larsson. 2007. Saproxylic beetle diversity in a managed boreal forest: importance of stands characteristics and forestry conservation measures. Diversity and Distributions **13:**418–429.

Meffe, G. and R. Carrol. 1997. Principles of Conservation Biology. Sinauer Press, Sunderland , MA.

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology **83:**1131–1145.

Müller, J., and M. Gossner. 2010. Three-dimensional partitioning of diversity reveals baseline information for state-wide strategies for the conservation of saproxylic beetles. Biological Conservation **143:**625–633.

Müller, J., and R. Bütler. 2010. A review of habitat thresholds for deadwood: a baseline for management recommendations in European forests. European Journal of Forest Research **129:** 981–992.

Müller, J., et al. 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography **38**: 499–509.

Nilsson, S. G., J. Hedin, and M. Niklasson. 2001. Biodiversity and its Assessment in Boreal and Nemoral Forests. Scandinavian. Journal of Forest Research (Suppl) **3:**10–26.

Olsson, J., T. Johansson. B. G. Jonsson, J. Hjalten, M. Edman, and L. Ericson. 2012. Landscape and substrate properties affect species richness and community composition of saproxylic beetles. Forest Ecology and Management **286:**108–120.

ONF. 2011. Bilan patrimonial des Forêts Domaniales hors DOM. ONF, Paris.

Ovaskainen, O. 2002. Long-Term Persistence of Species and the SLOSS Problem. Journal of Thoretical Biology **218:**419–433.

Parviainen, J., K. Kassiounis, W. Bücking, E. Hochbichler, R. Päivinen, and D. Little. 2000. Forest reserves research network in Europe. The Finnish Forest Research Institute, Joensuu Research Station.

Pernot, C., Y. Paillet, V. Boulanger, N. Debaive, M. Fuhr, O. Gilg, and F. Gosselin. 2013. Impact de l'arrêt d'exploitation forestière sur la structure dendrométrique des hêtraies mélangées en France. Revue Forestiere Francaise **65**: 445–461.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rabinowitz, D. 1981. Seven forms of rarity. Pages 205–217 in H. Synge, editor. The biological aspects of rare plants conservation. Wiley, New York.

Ranius, T., and L. Fahrig. 2006. Targets for maintenance of deadwood for biodiversity conservation based on extinction thresholds. Scandinavian Journal of Forest Research **21:**201–208.

Ranius, T., and O. Kindvall. 2006. Extinction risk of wood-living model species in forest landscapes as related to forest history and conservation strategy. Landscape Ecology **21:**687–698.

Ranius, T., P. Martikainen, and J. Kouki. 2011. Colonisation of ephemeral forest habitats by specialised species: beetles and bugs associated with recently dead aspen wood. Biodiversity and Conservation **20**: 2903–2915.

Riedinger, V., M. Renner, M. Rundlöf, I. Steffan-Dewenter, and A. Holzschuh. 2014. Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. Landscape Ecology **29**: 425–435.

Rotheray, E.L., L.F. Bussière, P. Moore, L. Bergstrom, and D. Goulson. 2014. Mark recapture estimates of dispersal ability and observations on the territorial behaviour of the rare hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae). Journal of Insect Conservation **18**: 179–188.

Schwartz, M.W. 1999. Choosing the appropriate scale of reserves for conservation. Annual Review of Ecology and Systematics **30**: 83–108.

Seibold, S., R. Brandl, J. Buse, T. Hothorn, J. Schmidl, S. Thorn, and J. Müller. 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conservation Biology **29**: 382–390.

Shmida, A., and S. Ellner. 1984. Coexistence of plant species with similar niches. Vegetation **58:**29–55.

Tjørve, E. 2010. How to resolve the SLOSS debate: Lessons from species-diversity models. Journal of Theoretical Biology **264:** 604–612.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecological Research **17:**229–239.

Wiktander, U., O. Olsson, and S. Nilsson. 2001. Seasonal variation in home range size, and habitat area requirement of the lesser spotted wood pecker *Dendrocopos minor*. Biological Conservation **100:**387–395.

Author Queries

Q1: Author: Please confirm that given names (red) and surnames/family names (green) have been identified correctly.
Q2: Author: Please complete the Color and Page charge form included with your proofs and return within 7 days. If you have questions regarding page or color charges, please contact CBI@wiley.com.
Q3: Author: The conjunction *and* (highlighted) in the sentence "Abundance of rare . . . " cannot be replaced by a comma. Please check.
Q4: Author: Please check whether the edits made in the sentence "Spillover and habitat amount . . . " are okay.
Q5: Author: A running head short title was not supplied; please supply a short title that can be used instead.
Q6: Author: Please cite Table 2 in the text.
Q7: Author: Please check if the following number is supposed to be 0.01; there are two 0.001s provided.
Q8: Author: Please check whether the edits made from the sentence "In all our other study sites . . . " till the last line of the subsection are okay.
Q9: Author: Please check if the definition of ∗∗ (highlighted) is correct as set in the caption of Figure 2.

Article 9: PASSIFOR: A reference library of DNA barcodes for French saproxylic beetles (Insecta, Coleoptera)

Biodiversity Data Journal 3: e4078
doi: 10.3897/BDJ.3.e4078

Data Paper

PASSIFOR: A reference library of DNA barcodes for French saproxylic beetles (Insecta, Coleoptera)

Rodolphe Rougerie[‡,§], Carlos Lopez-Vaamonde[§], Thomas Barnouin[|], Julien Delnatte[¶], Nicolas Moulin[#], Thierry Noblecourt[|], Benoît Nusillard[¤], Guillem Parmain[¤], Fabien Soldati[|], Christophe Bouget[¤]

‡ Muséum national d'Histoire Naturelle, Sorbonne Universités, Institut de Systématique, Évolution, Biodiversité (ISYEB), UMR 7205 – CNRS, MNHN, UPMC, EPHE, Paris, France
§ INRA UR633 Zoologie Forestière, Orléans, France
| Office National des Forêts (ONF), Laboratoire National d'Entomologie Forestière, Quillan, France
¶ Independent researcher, Avignon, France
# Entreprise Nicolas Moulin Entomologiste, Bihorel, France
¤ IRSTEA Ecosystèmes Forestiers, Nogent-Sur-Vernisson, France

Corresponding author: Rodolphe Rougerie (rodolphe.rougerie@mnhn.fr)

Academic editor: Axel Hausmann

Received: 17 Sep 2014 | Accepted: 24 Feb 2015 | Published: 04 Mar 2015

Citation: Rougerie R, Lopez-Vaamonde C, Barnouin T, Delnatte J, Moulin N, Noblecourt T, Nusillard B, Parmain G, Soldati F, Bouget C (2015) PASSIFOR: A reference library of DNA barcodes for French saproxylic beetles (Insecta, Coleoptera). Biodiversity Data Journal 3: e4078. doi: 10.3897/BDJ.3.e4078

Abstract

Saproxylic beetles – associated with dead wood or with other insects, fungi and microorganisms that decompose it – play a major role in forest nutrient cycling. They are important ecosystem service providers and are used as key bio-indicators of old-growth forests. In France alone, where the present study took place, there are about 2500 species distributed within 71 families. This high diversity represents a major challenge for specimen sorting and identification.

The PASSIFOR project aims at developing a DNA metabarcoding approach to facilitate and enhance the monitoring of saproxylic beetles as indicators in ecological studies. As a first step toward that goal we assembled a library of DNA barcodes using the standard genetic marker for animals, i.e. a portion of the COI mitochondrial gene. In the present contribution, we release a library including 656 records representing 410 species in 40 different families. Species were identified by expert taxonomists, and each record is linked

to a voucher specimen to enable future morphological examination. We also highlight and briefly discuss cases of low interspecific divergences, as well as cases of high intraspecific divergences that might represent cases of overlooked or cryptic diversity.

Keywords

DNA barcoding, COI, molecular identification, cryptic diversity, Coleoptera, forest insects, ecological indicators.

Introduction

Forests ecosystems cover nearly 30% of the total land surface globally and host most of the terrestrial biodiversity. They are highly complex systems whose functioning and sustainability depends on a range of spatially and temporally dynamic abiotic and biotic factors. To monitor or diagnose forest ecosystems, ecologists have historically used both physico-chemical and biological indicators. Among the latters, saproxylic beetles – associated with dead wood or with other insects, fungi and microorganisms that decompose it – have been used as key bio-indicators of old-growth forests in both temperate and boreal regions of the globe (but see Grove and Stork (1999) for perspectives toward their monitoring in tropical forests). Their diversity is high (several hundred species co-occur in most forests), they can be abundant, and samples are generally easily collected using standard techniques facilitating comparisons between sites. Saproxylic beetle species include both generalists and highly specialized organisms, sometimes requiring complex and stringent conditions in order to fulfill their development and reproduction. As a consequence, their communities have been shown to be tightly linked to the features and the dynamics of the habitat (Grove 2002).

In conservation biology studies, saproxylic beetles have often been studied through the perspective of focal species (often endangered/patrimonial species (e.g. Buse et al. 2007)), and of communities (e.g. Bouget et al. 2014, Buse et al. 2010, Lassauce et al. 2013, Quinto et al. 2012), considering the presence/absence of the former, and/or the diversity and relative abundances of species within the latter. However, these studies are strongly impeded by the considerable diversity of these insects. In France alone, there are about 2500 species distributed within 71 families, and several hundreds of specimens representing dozens of species can be collected in a single trap (see Bouget et al. (2009) for details about standard collecting methods using interception traps). Because of this diversity and abundance, and because species identification using morphology requires strong and rather scarce taxonomic expertise, specimen sorting and identification represent the main bottleneck in studies of saproxylic beetles, thus impeding their consideration in large-scale forest biodiversity monitoring schemes.

DNA-based identification, and the development of metagenomic approaches using Next Generation Sequencing (NGS) technologies, hold strong promise to overcome this

impediment and may alleviate funding and time constraints for large-scale studies on these insects. Molecular identification of species has seen a considerable and rapid development over the past decade following the introduction of DNA barcoding by Hebert et al. (2003); during this period, the field has experienced extensive testing in a large variety of organisms, including many insect orders. DNA barcode libraries are being developed at a steady pace, combining genetic data (usually the sequences of the genetic marker used as the standard DNA barcode in animals: a 658bp fragment of the mtDNA COI gene, although additional markers are sometimes used to complement it), taxonomic information, and specimen data (collecting information, voucher repository, images). A global online database, the Barcode of Life Datasystems (BOLD), serves as the central repository for these libraries (www.boldsystems.org) and combines classical database features with a workbench facilitating data analyses and data sharing (Ratnasingham and Hebert 2007). At the same time, advances in NGS technologies have increased by several orders of magnitude the yield and throughput of DNA sequencing and triggered the development of metagenomics. Multiple genomes can now be extracted, amplified and sequenced simultaneously, allowing for the sequencing of environmental (air, water or soil for instance) or bulk (complex assemblages of multiple individuals) samples (Shokralla et al. 2012, Tautz et al. 2010). By targeting a DNA marker that permits species identification, like DNA barcodes, this method can be used to document the species composition of complex samples, like communities, in an approach called DNA metabarcoding (Hajibabaei et al. 2011, Taberlet et al. 2012, Yu et al. 2012, Cristescu 2014).

The PASSIFOR project, initiated by the National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA) and by the National Institute for Agricultural Research (INRA), aims at developing a DNA metabarcoding approach for French species of saproxylic beetles to facilitate and enhance the use of these insects as forest indicators. As a first step toward that goal, we present and release in this paper a DNA barcode reference library for these insects, including 656 records representing 410 species in 251 genera and 40 different families. This library represents about 16% of the national fauna and we expect that its development in the next future will further contribute to the assembly of a DNA barcode library for European beetles. Remarkable progress was recently accomplished toward that goal with the published results of national campaigns in Finland (Pentinsaari et al. 2014) and in Germany (Hendrich et al. 2014) together representing 4330 species with DNA barcodes in Northern and Central Europe.

General description

Purpose: This library aims to provide an authoritative reference library for the DNA-based species identification of French saproxylic beetles, in order to facilitate the use of DNA metabarcoding in biodiversity monitoring networks focusing on these forest insects. It is also expected to develop the use of DNA barcodes by the community of coleopterists, in combination with characters from the morphology, ecology and biogeography of species, to address taxonomic questions.

Addititional information: Because the available funding for this project was too limited to develop an exhaustive library for French saproxylic beetles (ca. 2500 species) or to allow the documentation of intraspecific and geographical patterns of genetic variation, our initial objective has been to target a broad taxonomic coverage, favoring taxonomic diversity at the family, genus and species levels. Only a few species complex or notoriously difficult genera (e.g. *Ampedus* in family Elateridae) were more densely sampled.

The PASSIFOR library uses the standard DNA barcode for animals, i.e. a 658bp fragment of the COI mitochondrial gene.

Species identifications were provided by expert taxonomists for these groups. All records were initially identified on the basis of morphological examination, and voucher specimens are preserved in the collections of the taxonomists as references for these records. Any future change in the taxonomy/nomenclature of these insects will be reported in the PASSIFOR library, after authoritative validation by the taxonomists.

Project description

Title: PASSIFOR: stands for (in French) "Proposition d'Amélioration du Système de Suivi de la bIodiversité FORestière": Proposal toward improving monitoring of forest biodiversity.

Personel: *PIs*: Christophe Bouget (IRSTEA, Nogent-Sur-Vernisson) & Carlos Lopez-Vaamonde (INRA, Orléans)

Postdoctoral fellow: Rodolphe Rougerie (INRA, Orléans)

Study area description: Western Europe: France (99.1% of the samples), Czech Republic, Italy, Spain, and Morocco.

Funding: This project is supported by a grant from the French Ministry of Agriculture (MAAF) to IRSTEA (CB) and INRA (CLV). Sequencing of DNA barcodes also benefitted from funding by Genome Canada and the Ontario Genomics Institute (OGI) to the International Barcode of Life Project (iBOL).

Sampling methods

Study extent: The PASSIFOR library focuses on French species within 40 different families of saproxylic beetles.

Sampling description: Tissue samples for DNA extraction were collected mostly from dry collection specimens; only a limited number of samples were preserved in 95%-ethanol. All specimens were photographed and specimen data were compiled in excel spreadsheets for submission to BOLD.

Most specimens were sampled by RR and CLV in the National Laboratory for Forest Entomology, Quillan, France. GP, TB and BN assisted in sampling and in databasing records in their institutional collections. NM sampled specimens in his own reference collection, while JD selected and shipped a selection of specimens (Elateridae, especially members of genus *Ampedus*) to INRA Orleans where RR handled tissue sampling, photography and databasing.

Quality control: All tissue samples were assembled in 96-well plates in which one well (location H12) was left empty to serve as a negative control. After sequencing and upload of sequences into BOLD, DNA barcodes were compared through classical analyses of genetic distances (blast hits, NJ trees) to conspecific records, when existing, in other accessible DNA barcoding projects/campaigns. Discordances between DNA results and taxonomy derived from morphology (DNA barcodes shared by distinct species, deep intra-specific splits (>2%)) led to re-examination of the specimens; collegial discussions were initiated to address these issues by revealing possible cases of mis-identification or cross-contamination.

Step description: The construction of the PASSIFOR library can be divided into two main steps:

1. *Specimen sampling and data compilation*:
    - tissue sampling. Using flame-decontaminated forceps, we usually pulled one leg from each specimen sampled. Occasionally, when these appendages were difficult to reach, we used the antenna or hindwing of the insect. For the smallest species, we sometimes used up to three of these body parts (usually several legs). Only in one case, a tiny representative of the Scolytinae *Ernoporicus fagi*, did we use the whole insect and as a consequence did not preserve any voucher specimen.
    - photography. Each specimen was photographed individually along with a scale.
    - data compilation. We used standard BOLD spreadsheets to compile:
        - voucher information: SampleID (a unique BOLD identifier for the specimen; also added on a label pinned with the voucher specimen) and institution storing.
        - Taxonomy data: higher level taxonomy; species identification; identifier, including contact information.
        - Specimen details: sex (when available); reproduction mode; life stage; type of tissue used (for most specimens); collecting method (when available).
        - Collection data: collectors; date collected; country; administrative region and department; sector; exact site; latitude, longitude and elevation (when available).
    - upload to BOLD. Following the standard BOLD procedure for DNA barcode library construction, we created a dedicated project in BOLD. This project (code PSFOR, publicly accessible) hosts records for all the samples processed (including failures), whereas the actual PASSIFOR library

(dataset DS-PSFOR01, see the *Data resources* section below) only includes records successfully sequenced and subsequently validated by taxonomists.

2. *Sequencing of DNA barcodes*: The Canadian Centre for DNA Barcoding (CCDB), hosted by the Biodiversity Institute of Ontario (BIO) at the University of Guelph, Ontario, Canada) processed the tissue samples; all operations were carried out following the standard high-throughput protocols in place at CCDB and available from http://ccdb.ca/resources.php. For PCR amplification, we used a primer cocktail combining the LCO1490/HCO2198 pair (Folmer et al. 1994) with the LepF1/LepR1 pair (Hebert et al. 2004) for amplification of the full-length (658bp) DNA barcode region of the COI gene. Samples failing to amplify with these primers were alternatively processed using internal primers targeting shorter fragment; MLepR2 (Hebert et al. 2013) was used along with LCO1490/LepF1, and MLepF1 (Hajibabaei et al. 2006) was used with HCO1498/LepR1 to target fragments of 307bp and 407bp, respectively. Unpurified PCR fragments were sequenced in both directions using an ABI 3730XL DNA Analyzer (Applied Biosystems, Foster City, CA, USA). CodonCode (CodonCode Corporation, Centerville, MA) was used for trimming primers, contig assembly and sequence editing; alignment was straightforward in absence of indels and the sequences, along with corresponding trace files, were uploaded to BOLD.

Geographic coverage

Description: The PASSIFOR library covers 17 of the 22 administrative regions of France, including Corsica. The map in Fig. 1 represents the distribution of the PASSIFOR records.

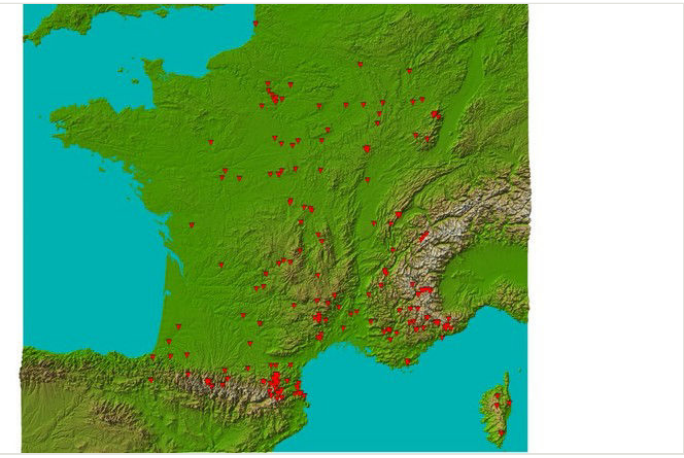


Figure 1.

Distribution of the PASSIFOR library records (Suppl. material 1).

Coordinates: 41.7 and 50.5 Latitude; -1.6 and 9.5 Longitude.

Taxonomic coverage

Description: The PASSIFOR library comprises 656 records for saproxylic beetles belonging to 40 different families. They represent 410 species in 251 genera. Table 1 provides the details on sampling for each family.

Table 1.

Taxonomic coverage of the PASSIFOR library giving details of the number of records, genera and species sampled within each of the 40 families included (ordered alphabetically).

Family	Records	Genera	Species
Anthribidae	11	9	9
Biphyllidae	2	1	1
Bostrichidae	1	1	1
Brentidae	1	1	1
Buprestidae	7	6	7
Cerambycidae	165	69	115
Cerophytidae	1	1	1
Ciidae	1	1	1
Cleridae	12	5	6
Curculionidae	54	19	31
Elateridae	151	22	57
Endomychidae	2	1	1
Erotylidae	2	2	2
Eucinetidae	1	1	1
Eucnemidae	8	4	5
Histeridae	1	1	1
Laemophloeidae	2	2	2
Leiodidae	3	2	2
Lucanidae	8	4	4
Lycidae	6	5	5
Lymexylidae	4	2	2

Melandryidae	24	12	16
Monotomidae	9	1	7
Mycetophagidae	15	4	11
Nitidulidae	7	3	6
Nosodendridae	1	1	1
Oedemeridae	11	4	8
Prostomidae	1	1	1
Ptinidae	30	12	23
Pyrochroidae	5	2	3
Pythidae	1	1	1
Salpingidae	14	6	11
Scarabaeidae	16	5	14
Silvanidae	2	2	2
Sphindidae	2	2	2
Tenebrionidae	51	21	32
Tetratomidae	1	1	1
Trogidae	2	1	1
Trogossitidae	14	8	9
Zopheridae	7	5	6
Total	**656**	**251**	**410**

The nomenclature used generally follows that in the eight volumes of the Catalogue of Palaearctic Coleoptera series, edited by Löbl and Smetana (see f.i Löbl and Smetana (2003)), which in turn was largely followed, for French beetles, in the recent national catalogue by Tronquet (2014). New names and nomenclatural changes after publication of the volumes of the Löbl & Smetana catalogue were sometimes adopted in the PASSIFOR library, but only if they did not conflict with other DNA barcode libraries for these insects, or if they are considered consensual within the community of coleopterists involved in the construction of these libraries. This strategy favors the consistency of names used within several independently constructed libraries in BOLD rather than an authoritative stand for one or another of alternative names. This should prevent, or at least limit, the existence of "parallel taxonomies" (multiple names or combination of names for a single species) in BOLD.

Usage rights

Use license: Open Data Commons Attribution License

Data resources

Data package title: PASSIFOR DNA barcode reference library

Resource link: http://dx.doi.org/10.5883/DS-PSFOR01

Alternative identifiers: PASSIFOR library

Number of data sets: 1

Data set name: DS-PSFOR01

Download URL: http://www.boldsystems.org/index.php/Public_BINSearch?searchtype=records

Data format: xml, tsv, fasta, ab1

Description: The PASSIFOR library dataset can be downloaded from the Public Data Portal of BOLD in different formats (data as xml or tsv files, sequences and trace files as fasta and ab1 files). Alternatively, BOLD users can login and access the dataset via the Workbench platform of BOLD (see the public dataset list in the User Console page, under the name of first author); all records are also searchable within BOLD using the search function of the database.

The version of the library at the time of writing of this manuscript is also included as Suppl. materials 1, 2 in the form of an excel spreadsheet for record information and of a fasta file containing all aligned sequences.

Column label	Column description
processid	Unique identifier for the DNA sample.
sampleid	Unique identifier for the specimen and by extension the tissue sample used for DNA analysis.
recordID	Entry number in the database.
catalognum	Identifier for specimen assigned by formal collection upon accessioning.
fieldnum	Identifier for specimen assigned in the field.
institution_storing	The full name of the institution that has physical possession of the voucher specimen.
bin_uri	URI (Unique Resource Identifier) for the Barcode Index Number (BIN) to which the record belongs.

phylum_taxID	Taxonomic identifier of level Phylum
phylum_name	Phylum name
class_taxID	Taxonomic identifier of level Class
class_name	Class name
order_taxID	Taxonomic identifier of level Order
order_name	Order name
family_taxID	Taxonomic identifier of level Family
family_name	Family name
subfamily_taxID	Taxonomic identifier of level Subfamily
subfamily_name	Subfamily name
genus_taxID	Taxonomic identifier of level Genus
genus_name	Genus name
species_taxID	Taxonomic identifier of level Species
species_name	Species name
identification_provided_by	Full name of primary individual who assigned the specimen to a taxonomic group.
voucher_type	Status of the specimen in an accessioning process.
tissue_type	A brief description of the type of tissue or material analyzed.
collectors	The full or abbreviated names of the individuals or team responsible for collecting the sample in the field.
collectiondate	The date during which the sample was collected.
collectiondate_accuracy	A numerical representation of the precision of the Collection Date given in days and is represented as +/- the value.
lifestage	The age class or life stage of the specimen at the time of sampling.
sex	The sex of the specimen.
reproduction	The presumed method of reproduction.
extrainfo	A brief note or project term associated with the specimen for rapid analysis.
notes	General notes regarding the specimen.
lat	The geographic latitude (in decimal degrees) of the geographic center of a location.
lon	The geographic longitude (in decimal degrees) of the geographic center of a location.
coord_source	The source of the latitude and longitude measurements.

coord_accuracy	A decimal representation of the precision of the coordinates given in the decimalLatitude and decimalLongitude.
elev	Elevation of sampling site. Measured in meters relative to sea level. Negative values indicate a position below sea level.
depth	For organisms collected beneath the surface of a water body. Measured in meters below surface of water.
elev_accuracy	A numerical representation of the precision of the elevation given in meters and is represented as +/- the elevation value.
depth_accuracy	A numerical representation of the precision of the depth given in meters and is represented as +/- the depth value.
country	The full, unabbreviated name of the country, major political unit, or ocean in which the organism was collected.
province	The full, unabbreviated name of the state, province, territory, or prefecture (i.e., the next smallest political region below Country) in which the organism was collected.
region	The full, unabbreviated name of the county, shire, municipality, or park (i.e., the next smallest political region below province/state) in which the organism was collected.
sector	The full, unabbreviated name of the lake, conservation area or sector of park in which the organism was collected.
exactsite	Additional text descriptions regarding the exact location of the collection site relative to a geographic or biologically relevant landmark.

Additional information

In the following sections we provide a quick description of the results of DNA barcode analyses as carried out using the analytical tools available through the BOLD's workbench at the time of writing of this manuscript.

Sequence composition

The summary statistics for nucleotide frequency distribution are provided in Table 2. The range of variation in GC content (26 - 47%) within our very diverse set of taxa (40 families) is large and similar to previous reports in insects (Clare et al. 2008). It is most variable at the 1st (34.6 - 54.7%) and 3rd (1.9 - 43.8%) codon positions.

Table 2.

Nucleotide frequency distribution for sequences (>400bp, 597 sequences analyzed) in the PASSIFOR library.

	Min	Mean	Max	SE
G %	13.37	16.17	21.73	0.04
C %	12.61	19.82	27.68	0.13
A %	25.31	29.74	34.15	0.06
T %	26.44	34.26	44.07	0.15
GC %	25.99	35.99	46.81	0.14
GC % Codon Pos 1	34.65	46.84	54.72	0.13
GC % Codon Pos 2	38.3	42.65	46.44	0.04
GC % Codon Pos 3	1.94	18.43	43.77	0.31

Analyses of genetic distances

All sequence analyses were carried out in BOLD using Kimura-2 parameters (K2P) distances with BOLD handling the sequence alignment. Alternative alignment methods were tested (including the use of sequences aligned "as uploaded") and proved to have no impact on the results.

All 656 sequences of the library where used to build a Neighbor-Joining (NJ) tree as illustrated in Suppl. material 3. For the analysis of intraspecific and interspecific distances, we reduced the dataset to sequences longer than 400bp (597 records, 388 species). General summary statistics at the species, genus and family levels are given in Table 3; Fig. 2 shows the frequency distributions of genetic distances within species (normalized) and within genus. Fig. 3 represents the distribution of maximum intraspecific distances (singletons excluded) plotted against distances to Nearest Neighbour within the library. Overall, we observe a conspicuous bimodal pattern suggesting the existence of a marked "barcode gap" between intraspecific and interspecific genetic divergence. We note however that in the vast majority of species our sampling remains too limited, both taxonomically (sister species often unsampled) and numerically (intraspecific divergence undocumented for most species) to test the extent of this gap and its consistency.

Table 3.

Summary of distance (K2P) variations at species, genus and family levels, as calculated with BOLD from 597 records of the PASSIFOR library with DNA barcodes longer than 400bp.

	n	Taxa	Comparisons	Min Dist(%)	Mean Dist(%)	Max Dist(%)	SE Dist(%)
Within Species	334	125	458	0	0.85	14.93	0

Within Genus	362	73	3152	0	12.5	27.14	0
Within Family	573	25	20617	9.54	21.9	39.13	0

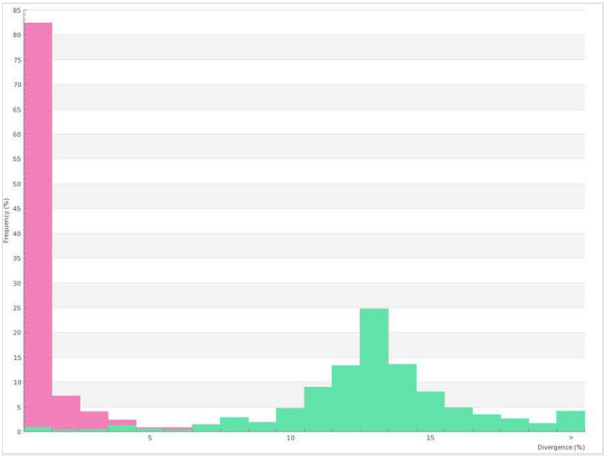


Figure 2.

Frequency distribution of within-species (normalized, in pink) and within-genus (green) K2P distances for records of the PASSIFOR library (sequences longer than 400 bp only: 597 records, 388 species). Table of distances is provided as Suppl. material 4 and Suppl. material 5.

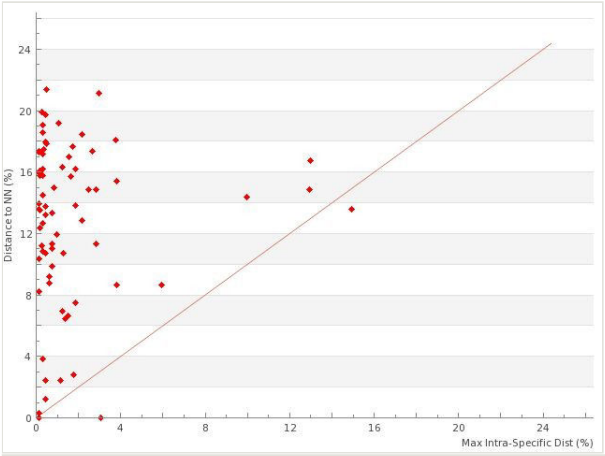


Figure 3.

Scatterplot representing for each species of the PASSIFOR library (sequences longer than 400 bp only: 125 species after exclusion of singletons) the minimum distance to Nearest Neighbour (NN) plotted against the maximum intra-specific distance (Suppl. material 6).

Discrepancies between current taxonomy and DNA barcode results

While we are aware of the limitation of our dataset to address taxonomic questions in cases where DNA barcodes and current taxonomy reveal a possible discordance, we report here two categories of apparent conflicts between the results from DNA barcode analyses and species identifications derived from morphology.

1. High intraspecific divergence (>2%) were observed in 7 species (Table 4). All these cases require further sampling and investigation to figure if they represent cases of overlooked or cryptic diversity, or if they may represent geographical population structure, ancestral polymorphisms, or variation resulting from *Wolbachia* infections (Smith et al. 2012). As an example, in the Tenebrionidae *Nalassus ecoffeti*, where intraspecific genetic distance is as high as 13.2%, our results suggest the possible validity of the currently synonymized Pyrenean species *N. temperei* Ardoin, 1958 (F. Soldati, personal communication).
2. Low interspecific divergences (<2%) were observed in 6 pairs of species, 1 triplet, and 2 pairs of subspecies (Table 5). In total, of the 410 species sampled in the PASSIFOR library, 15 (3.6%) fall in this category of low to null interspecific distances. Here again, these cases will require additional sampling and further investigation to understand if our results reflect cases of overlooked synonymy (as may be the case in the pairs *Ampedus pomorum* / *A. nemoralis*, *Anastrangalia dubia* / *A. reyi* (the second originally described as a mere variety of the former)), introgression through past or ongoing hybridization, or recent speciation resulting in low level of divergence (e.g. in the pairs *Pityophagus ferrugineus* / *P. laevior* and *Ampedus pomonae* / *A. sanguinolentus*). In fact, our results only revealed two cases of strictly shared DNA barcodes (one pair and one triplet within the taxonomically difficult genus *Ampedus*), although results for Central European samples of *Anastrangalia dubia* and *A. reyi* (Hendrich et al. 2014) confirmed that the two species cannot be distinguished using their DNA barcodes.

Table 4.

List of species within the PASSIFOR library (sequence length>400 bp; 597 records, 388 species) with more than 2% intraspecific divergence (N = number of records).

Family	Species	N	Max. Intrasp. (%)
Cerambycidae	*Alosterna tabacicolor*	3	11.2
Cerambycidae	*Tetrops praeustus*	2	11.8
Cleridae	*Thanasimus formicarius*	2	11.5
Cleridae	*Tillus elongatus*	4	8.8
Elateridae	*Melanotus castanipes*	2	5.7
Elateridae	*Melanotus villosus*	3	4.5
Tenebrionidae	*Nalassus ecoffeti*	5	13.2

Table 5.

List of species and subspecies pairs/triplet within the PASSIFOR library for which the minimum distance to the nearest heterospecific or heterosubspecific record is below 2% (number of records for each taxon is given within brackets next to its name).

Family	Species pairs & triplet	Min. intersp. (%)
Cerambycidae	*Anastrangalia dubia* (3) / *A. reyi* (1)	0.47
Cerambycidae	*Chlorophorus ruficornis* (1) / *C. sartor* (1)	1.1
Cerambycidae	*Paracorymbia hybrida* (1) / *P. maculicornis* (1)	0.92
Elateridae	*Ampedus cardinalis* (3) / *A. praestus* (2) / *A. melonii* (1)	0
Elateridae	*Ampedus pomonae* (1) / *A. sanguinolentus* (1)	1.61
Elateridae	*Ampedus pomorum* (9) / *A. nemoralis* (3)	0
Lucanidae	*Lucanus cervus* (1) / *L. cervus fabiani* (1)	0
Nitidulidae	*Pityophagus ferrugineus* (1) / *P. laevior* (1)	1.88
Scarabaeidae	*Protaetia cuprea* (1) / *P. cuprea metallica* (1)	1.22

Acknowledgements

We are thankful to Benoît Dodelin (Lyon, France) for providing additional material in genus *Ampedus*, and to Hervé Brustel and Lionel Valladares of the PURPAN Engineering School (Toulouse, France) for their discussions of taxonomic questions.

We also gratefully acknowledge the support from colleagues at the Canadian Centre for DNA Barcoding (University of Guelph, Ontario, Canada), and in particular Natalia Ivanova, Jayme Sones and Evgeny Zakharov who carefully and efficiently supervised the processing of the material analyzed in the present work.

Author contributions

Contributed to:

- Study design: CB, CLV, RR
- Specimen sampling, databasing: JD, CLV, NM, BN, GP, RR
- Sequence analyses: RR
- Taxonomic expertise, result validation: TB, CB, JD, NM, TN, BN, GP, FS
- Writing of manuscript: RR
- Editing/comments to the manuscript: TB, CB, JD, CLV, NM, TN, BN, GP, RR, FS

References

- Bouget C, Brustel H, Brin A (2009) Evaluation of window flight traps and ethanol lures for effectiveness at monitoring dead wood associated beetles. Agricultural and Forest Entomology 11: 143-152.
- Bouget C, Larrieu L, Brin A (2014) Key features for saproxylic biodiversity from rapid habitat assessment in temperate forests. Ecological Indicators 36: 656-664.
- Buse J, Schröder B, Assmann T (2007) Modelling habitat and spatial distribution of an endangered longhorn beetle – A case study for saproxylic insect conservation. Biological Conservation 137 (3): 372-381. DOI: 10.1016/j.biocon.2007.02.025
- Buse J, Levanony T, Timm A, Dayan T, Assmann T (2010) Saproxylic beetle assemblages in the Mediterranean region: Impact of forest management on richness and structure. Forest Ecology and Management 259 (8): 1376-1384. DOI: 10.1016/j.foreco.2010.01.004
- Clare EL, Kerr KCR, von Königslöw TE, Wilson JJ, Hebert PDN (2008) Diagnosing Mitochondrial DNA Diversity: Applications of a Sentinel Gene Approach. Journal of Molecular Evolution 66 (4): 362-367. DOI: 10.1007/s00239-008-9088-2
- Cristescu ME (2014) From barcoding single individuals to metabarcoding biological communities: towards an integrative approach to the study of global biodiversity. Trends in Ecology & Evolution in press: 1-6. DOI: 10.1016/j.tree.2014.08.001
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294-299.
- Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics 33: 1-23.
- Grove SJ, Stork NE (1999) The conservation of saproxylic insects in tropical forests: a research agenda. Journal of Insect Conservation 3: 67-74.
- Hajibabaei M, Janzen DH, Burns JM, Hallwachs W, Hebert PDN (2006) DNA barcodes distinguish species of tropical Lepidoptera . Proceedings of the National Academy of Sciences 103 (4): 968-971.
- Hajibabaei M, Shokralla S, Zhou X, Singer GA, Baird DJ (2011) Environmental barcoding: a next-generation sequencing approach for biomonitoring applications using river benthos. PLoS One 6 (4): e17497. [In eng]. DOI: 10.1371/journal.pone.0017497
- Hebert PDN, Cywinska A, Ball SL, deWaard JR (2003) Biological identifications through DNA barcodes. Proceedings of the Royal Society B: Biological Sciences 270: 313-321.
- Hebert PDN, Penton EH, Burns JM, Janzen DH, Hallwachs W (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator* . Proceedings of the National Academy of Sciences 101 (41): 14812-14817. DOI: 10.1073/pnas.0406166101
- Hebert PDN, Dewaard JR, Zakharov EV, Prosser SWJ, Sones JE, McKeown JTA, Mantle B, La Salle J (2013) A DNA 'barcode blitz': rapid digitization and sequencing of a natural history collection. PLoS One 8 (7): e68535. [In eng]. DOI: 10.1371/journal.pone.0068535
- Hendrich L, Morinière J, Haszprunar G, Hebert PDN, Hausmann A, Köhler F, Balke M (2014) A comprehensive DNA barcode database for Central European beetles with a

focus on Germany: adding more than 3500 identified species to BOLD. Molecular Ecology Resources n/a: n/a-n/a. DOI: 10.1111/1755-0998.12354

- Lassauce A, Larrieu L, Paillet Y, Lieutier F, Bouget C (2013) The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation lengths in a French oak high forest. Insect Conservation and Diversity 6 (3): 396-410. DOI: 10.1111/j.1752-4598.2012.00214.x
- Löbl I, Smetana A (2003) Catalogue of Palaearctic Coleoptera Volume I: Archostemata-Myxophaga-Adephaga . Apollo Books, Stenstrup, Denmark, 819 pp.
- Pentinsaari M, Hebert PDN, Mutanen M (2014) Barcoding Beetles: A Regional Survey of 1872 Species Reveals High Identification Success and Unusually Deep Interspecific Divergences. PLoS ONE 9 (9): e108651. DOI: 10.1371/journal.pone.0108651
- Quinto J, Marcos-Garcia MA, Diaz-Castelazo C, Rico-Gray V, Brustel H, Galante E, Mico E (2012) Breaking down complex Saproxylic communities: understanding sub-networks structure and implications to network robustness. PLoS One 7 (9): e45062. [In eng]. DOI: 10.1371/journal.pone.0045062
- Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology Notes 7 (3): 355-364. DOI: 10.1111/j.1471-8286.2007.01678.x
- Shokralla S, Spall JL, Gibson JF, Hajibabaei M (2012) Next-generation sequencing technologies for environmental DNA research. Mol Ecol 21 (8): 1794-805. [In eng]. DOI: 10.1111/j.1365-294X.2012.05538.x
- Smith MA, Bertrand C, Crosby K, Eveleigh ES, Fernandez-Triana J, Fisher BL, Gibbs J, Hajibabaei M, Hallwachs W, Hind K, Hrcek J, Huang D, Janda M, Janzen DH, Li Y, Miller SE, Packer L, Quicke D, Ratnasingham S, Rodriguez J, Rougerie R, Shaw MR, Sheffield C, Stahlhut JK, Steinke D, Whitfield J, Wood M, Zhou X (2012) *Wolbachia* and DNA Barcoding Insects: Patterns, Potential, and Problems. PLoS One 7 (5): e36514. DOI: 10.1371/journal.pone.0036514
- Taberlet P, Coissac E, Pompanon F, Brochmann C, Willerslev E (2012) Towards next-generation biodiversity assessment using DNA metabarcoding. Molecular Ecology 21: 2045-2050.
- Tautz D, Ellegren H, Weigel D (2010) Next generation molecular ecology. Mol Ecol 19 Suppl 1: 1-3. [In eng]. DOI: 10.1111/j.1365-294X.2009.04489.x
- Tronquet M (2014) Catalogue des Coléoptères de France. Association Roussillonnaise d'Entomologie, Perpignan, France, 1056 pp.
- Yu DW, Ji Y, Emerson BC, Wang X, Ye C, Yang C, Ding Z (2012) Biodiversity soup: metabarcoding of arthropods for rapid biodiversity assessment and biomonitoring. Methods in Ecology and Evolution 3 (4): 613-623. DOI: 10.1111/j.2041-210X.2012.00198.x

Supplementary materials

Suppl. material 1: PASSIFOR library - specimen and sequence data

Authors: Rougerie R, Lopez-Vaamonde C, Barnouin T, Delnatte J, Moulin N, Noblecourt T, Nusillard B, Parmain G, Soldati F, Bouget C
Data type: Record information - specimen data and sequence summary
Brief description: This excel spreadsheet includes information about all records in BOLD for the PASSIFOR library at the time of writing. It contains specimen data and sequence information, including GenBank accession numbers.
Filename: PASSIFOR library_AUG-04-2014_BOLD data.xls - Download file (744.50 kb)

Suppl. material 2: PASSIFOR library - DNA sequences

Authors: Rougerie R, Lopez-Vaamonde C, Barnouin T, Delnatte J, Moulin N, Noblecourt T, Nusillard B, Parmain G, Soldati F, Bouget C
Data type: Genomic data, DNA sequences
Brief description: Sequences in fasta format for the fragment of the COI mtDNA gene used as a standard DNA barcode in animals. Each sequence is identified by a chain of characters consisting of, in the following order and separated by pipes: processID, sampleID, species_name, DNA marker
Filename: PASSIFOR library_AUG-04-2014_sequences.fasta - Download file (458.92 kb)

Suppl. material 3: Neighbour Joining tree reconstructed from the 656 DNA barcodes of the PASSIFOR library.

Authors: Rougerie R, Lopez-Vaamonde C, Barnouin T, Delnatte J, Moulin N, Noblecourt T, Nusillard B, Parmain G, Soldati F, Bouget C
Data type: Distance tree
Brief description: NJ tree resulting from the analysis with BOLD of the 656 DNA barcode sequences of the PASSIFOR library. Parameters for tree reconstruction are as follow: distance model: K2P; alignment method: BOLD aligner; sequence length: >200 bp; pairwise deletion option; all three codon positions included.
Filename: PASSIFOR library_AUG-04-2014_NJ tree.pdf - Download file (67.73 kb)

Suppl. material 4: Pairwise K2P distances within species

Authors: Rougerie R, Lopez-Vaamonde C, Barnouin T, Delnatte J, Moulin N, Noblecourt T, Nusillard B, Parmain G, Soldati F, Bouget C
Data type: Genetic distances
Brief description: This table lists K2P distances for all pairwise comparisons between conspecific records in the PASSIFOR library (only DNA barcodes longer than 400bp); distances are calculated in BOLD (www.boldsystems.org).
Filename: PASSIFOR - Within species K2P.xls - Download file (85.50 kb)

Suppl. material 5: Pairwise K2P distances within genera

Authors: Rougerie R, Lopez-Vaamonde C, Barnouin T, Delnatte J, Moulin N, Noblecourt T, Nusillard B, Parmain G, Soldati F, Bouget C
Data type: Genetic distances
Brief description: For the PASSIFOR library (only DNA barcodes longer than 400bp), this table lists K2P distances for all pairwise comparisons between heterospecific records of the same genus; distances are calculated in BOLD (www.boldsystems.org).
Filename: PASSIFOR - Within genus K2P.xls - Download file (387.00 kb)

Suppl. material 6: Intra-specific distances and distances to nearest neighbor (NN)

Authors: Rougerie R, Lopez-Vaamonde C, Barnouin T, Delnatte J, Moulin N, Noblecourt T, Nusillard B, Parmain G, Soldati F, Bouget C
Data type: Genetic distances
Brief description: This table provides, for each species of the PASSIFOR library with sequences longer than 400bp, mean and maximum intraspecific distances (non-applicable (N/A) for species represented as singletons in our dataset) as well as the distance to nearest neighbor (NN) within the library and its identification.
Filename: Table_Sx_intraSP.xlsx - Download file (69.43 kb)

Guilhem PARMAIN

Contribution de différents éléments forestiers et non-forestiers de la Trame de Très Vieux Bois à la diversité des coléoptères saproxyliques

La disparition et la fragmentation d'habitat sont considérées comme des causes majeures de l'érosion de la biodiversité. Les forêts sont parmi les plus riches écosystèmes terrestres de la planète. La simplification structurelle et la disparition d'éléments d'habitats clés qui résultent de leur exploitation mettent en péril la biodiversité qu'elles abritent.

Grâce à l'analyse de différents jeux de données mutualisés entre plusieurs laboratoires et de deux jeux de données originaux générés par mes travaux, l'objectif de cette thèse est d'évaluer le rôle joué par plusieurs éléments de la Trame de Très Vieux Bois pour la diversité des coléoptères saproxyliques aux échelles locale et paysagère. L'effet des caractéristiques du milieu et la biodiversité associée aux ilots de vieillissement, réserves forestières et arbres isolés extra-forestiers ont été évalués.

En parallèle, nous avons conduit des explorations méthodologiques concernant la principale technique d'échantillonnage de notre modèle biologique. Nous avons mis en évidence les effets (i) forts de la réplication spatiale ou temporelle des dispositifs d'échantillonnage sur les données obtenues, mais (ii) négligeables de l'exclusion d'une famille couteuse en temps d'identification sur les résultats.

Nos résultats écologiques indiquent l'effet de l'arrêt d'exploitation sur la reconstitution des compartiments bois mort et dendromicrohabitats et des assemblages de coléoptères saproxyliques associés, au contraire de l'extension de rotation représentée par les ilots de vieillissement. D'importantes densités de réserves forestières dans le paysage (plus de 20%) semblent nécessaires pour une conservation efficace de la faune saproxylique. De plus, nous avons mis en évidence qu'une part importante des espèces saproxyliques est préférentiellement retrouvée sur des arbres solitaires, non-forestiers. La totalité de la faune saproxylique n'est donc pas abritée par la forêt. Ces structures non forestières représentent des éléments primordiaux à prendre en compte pour la sauvegarde de la biodiversité saproxylique.

Mots clés : Réserve forestière, ilot de vieillissement, coléoptère saproxylique, méthodologie, arbres isolés, conservation.

How elementary components of the saproxylic habitat network contribute to associated beetle diversity?

Habitat loss and fragmentation are considered as major threats to biodiversity in forests, one of the species-richest terrestrial ecosystems worldwide. The structural simplification and the loss of key habitat elements resulting from forest harvesting threaten forest biodiversity. Through the analysis of datasets shared between laboratories and two original datasets created during this thesis, I intended to evaluate the role for associated beetle diversity of several components of the saproxylic habitat network at local and landscape scales. The effect of local environmental variables has been evaluated and the biodiversity associated with ageing stands, forest reserves and isolated non-forest trees were explored.

In parallel, we have analyzed the main technique used to sample our study group. We highlighted (i) strong effects of spatial or temporal replication of sampling on data, but (ii) negligible effects of data simplification by excluding a time-expensive family on results.

We demonstrated significant effects of forest setting aside on the restoration, mainly of dead wood and tree microhabitats, but also on associated saproxylic beetle assemblages. Extended rotations in ageing stands did not provide such positive effects. Besides, we evidenced that a high density of forest reserves in the landscape (over 20%) seems necessary to efficiently favor the saproxylic fauna. In addition, we observed that a significant proportion of saproxylic species prefer non-forest solitary tree habitats. The whole saproxylic fauna is therefore not hosted by forests. These non-forest saproxylic structures have to be included in conservation strategies dedicated saproxylic biodiversity.

Key words : Forest reserve, extended rotation, saproxylic beetle, sampling methods, solitary trees, biodiversity conservation.

irstea

MUSÉUM NATIONAL D'HISTOIRE NATURELLE

Ministère de l'Écologie, du Développement durable, des Transports et du Logement

Office National des Forêts